PATTERNS OF DIVERSITY AND ECOLOGY IN PANAMANIAN BATS AT TWO ELEVATIONS

By

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PATTERNS OF DIVERSITY AND ECOLOGY IN PANAMANIAN BATS AT TWO ELEVATIONS

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Chair: Brian K. McNab
Major Department: Zoology

Neotropical bats are the most diverse mammals in terms of number of species and food habits. Bats show differential distribution in relation to season, elevation, habitat, and forest strata. This study compared temporal and spatial bat diversity and ecology patterns between a lowland forest and a cloud forest in western Pacific Panamá. Bat communities were sampled monthly for 3.5 years with mist nets set in pairs, one in the understory the other in the canopy; and complemented with a 3-month acoustic inventory. Data on climate and forest structure were measured in both sites.

Although both forests had similar annual and seasonal rainfall patterns, the cloud forest had higher annual and monthly amounts of rainfall; and lower mean, maximal, and minimal ambient temperatures. The lowland forest had a taller, more closed canopy with less understory cover than the cloud forest. Bats in the lowland community clearly differentiated as either understory or canopy bats. Bats in the cloud forest community were either canopy bats or used both strata equally. Some bat species departed from the 1:1 male to female proportion in both forests, whereas other species varied the sex ratio with forest type and season. Species richness did not vary with forest type or strata, whereas species abundance varied with both forest type and strata. Results also showed similar total abundance between sites, but not between strata. The cloud forest bat community had higher evenness and species diversity than the lowland bat community. Bat species richness and abundance varied with month, season, and year, and some of these temporal patterns varied with forests type and strata. Bats' use of forest strata varied with species and season. The results suggest that bat communities are influenced by different factors including climate, forest structure, food availability, and competition.

CHAPTER 1
GENERAL INTRODUCTION

Among tropical mammals, bats play important roles in the ecosystem because of their species richness, ecological diversity, large biomass, and mobility; and their functions as pollinators, seed dispersers, and predators of invertebrates and small vertebrates (Findley 1993). Because of these characteristics, bats are a promising group to examine for factors that influence diversity and ecological patterns in tropical habitats. Although the importance of tropical bats has long been recognized, few studies have been conducted on the community level (Kalko 1998). This limited database made it difficult to answer fundamental questions about the high species diversity of tropical bats and their functional significance in the ecosystem (Kalko 1998).

Bats are difficult to study because of their flying capacity, nocturnal behavior, high diversity, and relative taxonomic uncertainty (Findley 1993, Kalko 1998, Lim and Engstrom 2001). These difficulties have led to collection of data without standardized methods, thus limiting the potential for comparison among studies (Kalko 1998) and establishing a weak theoretical framework. Recent studies in the Neotropics show that published bat species lists are incomplete because sampling bias (Kalko *et al.* 1996a, Voss and Emmons 1996). Some bat species fly in canopy or over the forest, making it difficult to sample with one method. However, comparative studies are now being conducted to identify latitudinal and altitudinal patterns in bat diversity, to identify mechanisms that structure bat communities, and to evaluate bats as potential indicators of ecosystem conditions in human-disturbed habitats. To fill the gap in bat ecological theory, it is necessary to gather new data from standardized, long-term studies that integrate a variety of inventory methods (Kalko 1998). Because it is almost impossible to conduct experimental studies of bats on the community level, most studies rely on the comparative approach wherein general patterns can be identified by examining diversity and structure of species assemblages in different habitats (Kalko 1998).

The objective of this work is to examine how the diversity and ecological patterns of two bat communities in western Pacific Panamá (a lowland forest and a cloud forest) vary spatially and temporally. Bats show differential distribution in relation to season, elevation, habitat, and forest strata (Handley 1967, Bonaccorso 1979, Humphrey and Bonaccorso 1979, Bonaccorso and Humphrey 1984, Fleming 1991, Bernard 2001, Kalko and Handley 2001, Lim and Engstrom 2001). Studies showed that bat species richness in the Neotropics increases with rainfall and vegetation complexity in lowland forest, but decreases with elevation (Koopman 1978, Graham 1983, Fleming 1986a, Muñoz 1990, 1993, Patterson *et al.* 1996) and that bat communities may vary in species composition through the year (Bonaccorso and Humphrey 1984). I conducted a 3.5-year long-term study to gather behavioral and ecological information that allow me to compare patterns in species richness, abundance, sex ratio, and strata use between a lowland forest and a cloud forest bat community by year and season. To accomplish a more complete bat inventory, I complemented my long-term understory and canopy mist-netting inventory with 3 months of acoustic inventory.

Bats, like Neotropical bees and birds, or North American granivorous rodents (Karr and Freemark 1983, Brown and Kurzius 1989, Roubik 1992) may show differences in their species' response to environmental variability. Bats are often highly variable in their behavior regarding abiotic and biotic factors (Fenton 1990). In Chapter 2, I examine the influence of season and forest type on the bat vertical stratification and adult sex ratio in these two communities by concentrating the analysis on the most common species of nectarivorous and frugivorous bats. I gathered data on rainfall and ambient temperature as well as data in forest structure to discuss the possible influence of these factors on bat ecology. The purpose of Chapter 2 was to evaluate the advantages of long-term sampling in both strata to detect variation in bat strata use and sex ratio that may influence bat diversity.

Currently, our knowledge of patterns and processes in bat communities is poor because of the lack of standardized, long-term comparative studies (Kalko 1997). Previous studies have compared bat communities in terms of their biogeography, morphology, and ecology (Fleming 1986a, Findley 1993, Stevens and Willig 1999, 2000) using data collected in different years and with different methods. These sampling biases may limit the ability of these studies to detect ecological patterns. By extending previous one-year bat studies, I described in Chapter 3 the temporal and spatial patterns of bat species richness and abundance in these forests to understand the diversity patterns in bat communities. I also examined the ecological characteristics of species that correlate with distribution and abundance within and between sites, and compared the results from this study with results obtained in other Neotropical sites. I discussed guild composition and structure with the purpose of identifying how resource differentiation may influence bat diversity in these sites.

Studies of sympatric bats in Neotropical forests show that differentiation of food, habitat, or temporal resources (Bonaccorso and Humphrey 1984, Kalko 1995) promote the coexistence of ecologically similar species. Additionally, these studies showed that bat species, especially frugivores, seasonally fluctuate in their populations and switch strata, suggesting that these patterns can be widespread among bats and can operate as a mechanism of coexistence. In Chapter 4, I investigated the extent to which nectarivorous and frugivorous bat species differentiate in vertical and temporal components. I mainly focused on species of the highly diverse and abundant bat genera: *Artibeus*, *Sturnira*, and *Carollia*. Because body size may influence strata use, I examined the correlation of vertical stratification with species body mass.

CHAPTER 2
PATTERNS IN CLIMATE, VEGETATION, AND BAT ECOLOGY IN A LOWLAND FOREST AND A CLOUD FOREST IN PANAMA

Introduction

Terrestrial animal communities are shaped by physical and biological factors that influence the distribution and abundance of groups of insects, birds, and mammals (Wolda 1978, Karr and Freemark 1983, August 1983, Colinvaux 1986, Begon *et al.* 1990). The effects of these environmental factors have implications for the feeding behavior and reproductive ecology of animals and therefore are important factors to consider for the conservation and management of biological diversity (Karr *et al.* 1992). However, because studies of the influence of environmental variability have not been undertaken in a wide diversity of habitats, the development of general principles is difficult (Karr *et al.* 1992). For example, it is difficult to show that rainfall is more important than temperature in regulating animal populations (Grant and Grant 1989).

Neotropical bats are an appropriate group to examine in studying the influence of environmental factors on animal ecology. They are exposed to contrasting environments at small and large spatio-temporal scales as a result of their life history, three-dimensional habitat, and wide distribution (Eisenberg 1981, Willig and Mares 1989, Findley 1993, Jones 2001). Furthermore, New World bats play important roles as pollinators, seeddispersers, and predators of invertebrates and small vertebrates in different habitats (Humphrey and Bonaccorso 1979, Fleming 1986, Willig and Mares 1989, Findley 1993, Kalko 1998). Bats have been considered good indicators of forest conditions because of their sensibility to forest disturbance (Johns *et al.* 1985, Fenton *et al.* 1992, Wilson *et al.* 1996, Medellin *et al.* 2000, Putz *et al.* 2000, Schulze *et al.* 2000). Consequently, it is important to identify differential ecological responses that may indicate changing habits if we are to understand and conserve forest habitats.

Neotropical bats differ in their distribution and abundance in respond to season, elevation, habitat, and forest strata (Bonaccorso 1979, Humphrey and Bonaccorso 1979, Bonaccorso and Humphrey 1984, Bernard 2001, Kalko and Handley 2001, Lim and Engstrom 2001). Furthermore, capture rates of some species show significant differences between understory and canopy nets (Kalko and Handley 2001). Changes in strata use are mainly related to tracking of food resources and changes in sex ratio may indicate reproductive constraints in one sex. These differences in behavior may be used as indirect evidence of differential foraging and reproductive behavior (Bonaccorso and Humphrey 1984, Fleming 1988, 1992, Gardner *et al.* 1991, Stoner 2001). For example, *Carollia perspicillata* in Costa Rica showed a male-skewed sex ratio during the dry season, a period of low food availability, when females migrate for energetic reasons to give birth in another site (Fleming 1988). In Panamá, the understory bat *C. perspicillata* switched to canopy fruits during the lactation period in the late rainy season (Bonaccorso and Humphrey 1984). Additionally, the sex ratio can give information about habitat change, social and reproductive structure, and survivorship (Fleming 1988, Estrada and Coates-Estrada 2001, Stoner 2002).

I intensively surveyed a lowland forest and a cloud forest for 3.5 years in western Panamá with the main objectives of determining if bats in these forests differentially use one stratum and if sex ratios change over time or between sites. This was accomplished by concentrating on the most common species of nectarivorous and frugivorous bats captured in these forests. Additionally, I measured rainfall, ambient temperature, and forest structure to see if these factors are related to variability of bat ecology.

Methods

Study Sites

This study was conducted at two sites in the province of Chiriquí, western Pacific Panamá (Figure 2-1). The lowland site was Cerro Batipa (8° 20' 14.4" N and 82° 15' 13.2" W, Figure 2-2), a private conservation area, with elevations ranging from 0 to 325 m. The site lies in a tropical moist forest life zone (Tosi 1969) and has a tropical climate with a prolonged dry season (McKay 2000 based on De Martonne 1964). This climate has a mean annual ambient temperature of 27.5º C, annual rainfall of < 2500 mm (McKay 2000), relatively constant precipitation from May to November, and a strong dry season from December to April. The vegetation covers 600 ha (Valdespino and Santamaria 1999) of tropical ombrophilous, semi-deciduous, and drought-deciduous forests (Mueller-Dombois and Ellenberg 1974). The forest has a gradient in disturbance conditions, from mature closed canopy to highly disturbed open canopy forest patches. Some forest edges border teak (*Tectona grandis*) plantations or mangroves. The forest has a canopy height of 30 m and emergent trees of 40 m, a closed canopy, and relatively open understory. The arboreal vegetation is dominated by *Anacardium excelsum*, *Ficus insipida*, *Ochroma pyramidale*, *Hymeneae courbaril*, among other species. In the lower stratum, the following taxa predominate: *Piper* spp., *Psycotria* spp., *Curatella americana*, *Faramea occidentalis*, and *Acacia collinsii* (Valdespino and Santamaria 1999).

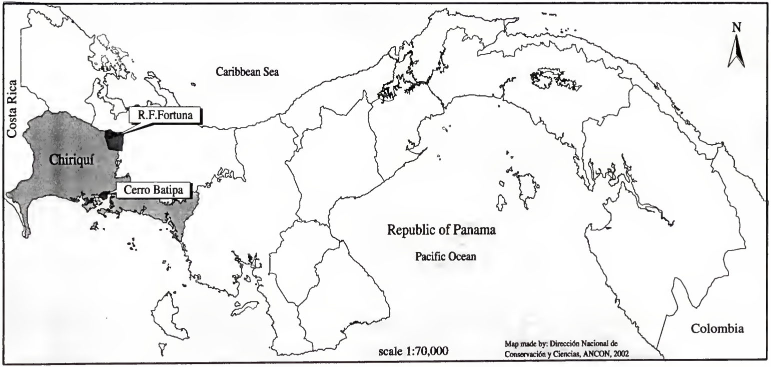
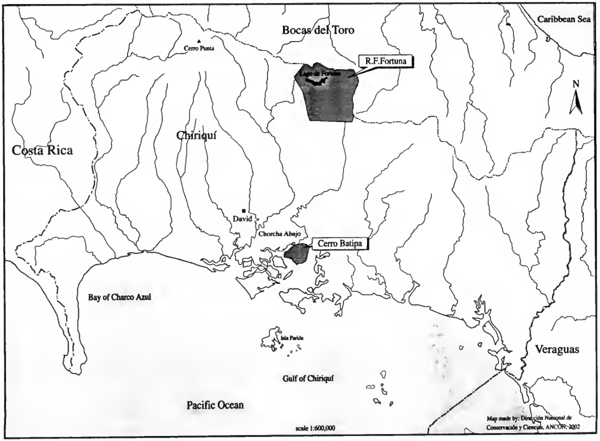


Figure 2-1. Location of the study region with the two study sites, Cerro Batipa and Reserva Forestal Fortuna in the Republic of Panamá. The study region is in the Province of Chiriquí, western Pacific Panamá.



Map made by: Dirección Nacional de Conservación y Ciencias, ANCON, 2002

Figure 2-2. Study sites are a lowland forest in Cerro Batipa and a cloud forest in the Reserva Forestal Fortuna. These forests are found along an elevational transect within the Gualaca Altitudinal Biological Corridor.

The cloud forest site was within the Fortuna Forest Reserve (8° 40'-8° 46'N, 82° 05'-82° 15'W, Figure 2-2), where the Smithsonian Tropical Research Institute (STRI) has a field station, and is 45 km from the lowland site. The reserve ranges in elevation from 800-2000 m (Díaz 1996), but the study site spans an elevational range of 1000-1400 m. Fortuna has two life zones (Tosi 1969, Díaz 1996), premontane wet forest and lower wet mountain forest. It shows a montane oceanic climate (McKay 2000 based on De Martonne 1964), with mean annual ambient temperature of 19ºC and annual rainfall of 3700 mm (Cavelier 1992, McKay 2000). The reserve comprises 19,500 ha of continuous lower mountain rainforest (Cavelier 1992, Diaz 1996), classified as a tropical ombrophilous (shade-tolerant) cloud forest (Mueller-Dombois and Ellenberg 1974). The forest canopy is 20-30 m in height, with an open canopy and emergent trees of 40 m, and a dense understory (Cavelier 1992). *Anthurium* and *Monstera* are abundant, as are vines and lianas, but there are few bromeliads. Epiphytic bryophytes are present, but are not as abundant as Araceae. Cyclanthaceae, Arecaceae, and Piperaceae are common in the understory, as well as tree ferns (Mayo *et al.* 1977, Cavalier 1992, Valdespino and Santamaria 1999, MacPherson 2000).

Both study sites are important for conserving biodiversity and establishing biological corridors in Panamá. Batipa is the second-largest remaining fragment of lowland forest in Chiriquí (Tovar 1996), and Fortuna is one of the best-preserved mountain forests in Panamá (Díaz 1994). Batipa and Fortuna are part of the proposed Gualaca Altitude Biological Corridor (Tovar 1996, Valdespino and Santamaria 1999). Fortuna is also part of the Central Cordillera Mountain Corridor (Tovar 1996).

Bat Mist Netting

Bats were monitored from July 1997 to December 2000, except for June 1998, when it was not possible to visit the sites. I sampled each bat community with mist nets for 1 to 4 nights monthly, depending on weather. Ten sampling stations were established in the lowlands and seven in the cloud forest. Each station was sampled for 1 to 2 nights with eight 2.5 x 12 m mist nets using Bonaccorso's (1979) "grid" arrangement (Kalko and Handley 2001). Nets were set in pairs at 20-50 m intervals, with one of each pair set at 0-3 m (understory) and the other at 6-15 m (subcanopy/canopy) in trails or natural openings in the vegetation (Figure 2-3). Nets were opened usually from sunset (1800 h) to midnight (2400 h) and checked every 30-60 min. Total sampling involved 8360 mist net hours (mnh) during 218 nights (lowlands 4060 mnh during 108 nights, cloud forest 4300 mnh during 110 nights).

Captured bats were placed in individual cloth bags, identified, marked, and released within 1 hour of capture. Bat species identification was based on keys for Panamanian lowland and western highland bats (C. Handley manuscripts) and a field guide of Central American mammals (Reid 1997). Only adult and subadult bats were marked (Chapter 3). I recorded species, sex, age, reproductive condition, forearm length, body mass, hour, and location (station, net number, and strata).

The use of mist nets to study bat or avian ecology has advantages and disadvantages (LaVal 1970, Fleming *et al.* 1972, Karr 1981, Kunz and Kurta 1988). Some advantages for assessing ecological information are that species can be properly identified, individuals can be measured, and their relative abundance can be estimated. Disadvantages are that capture rates are influenced by factors other than the relative abundance of the animal. These factors include weather, net location, variability in net

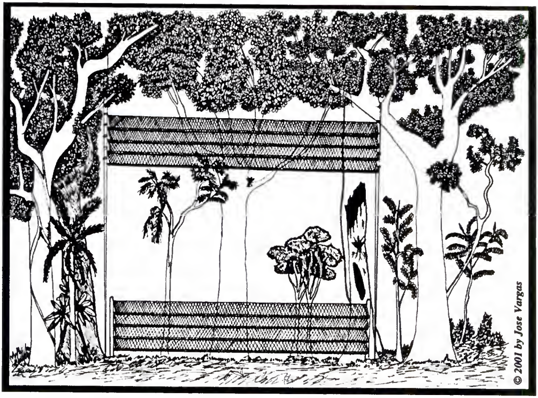


Figure 2-3. Arrangement of mist nets in sampling stations. Mist nets were set in pairs, one in the understory (0-3 m), the other in the canopy (6-15 m).

tension, habitat structure, differences in vertical movements and the proportion of time spent within the 2-m sampling zone, differences in flight distance, the ability of bats to detect the presence of nets, and differences in flight frequency (MacArthur and MacArthur 1974, Karr 1981, Kunz and Kurta 1988). Remsen and Good (1996) suggested long-term studies on marked individuals overcome some of these disadvantages. My study reduced some negative biases of mist nets because it was a long-term study (3.5 y), it sampled both understory and canopy, and used marked individuals.

Rainfall and Temperature Records

I obtained local records of rainfall and temperature data from the Empresa de Transmisión Electrica S. A. (ETESA) meteorological office (Fortuna Casa Control) and Facultad de Ciencias Agropecuarias (FCA), Universidad de Panamá, Chiriquí for cloud forest and lowland station, respectively. I have 4 years (1997-2000) of records for annual and monthly rainfall from the cloud forest (1010 m) and from Facultad de Ciencias Agropecuarias (35 m), which is 20 km from the study site in the lowlands. The records for ambient temperature (T_a) include 4 years (1997-2000) of annual and monthly means, maximal ($T_a$max), and minimal ($T_a$min) temperatures from FCA in the lowlands and the cloud forest.

Forest Structure Measurements

I measured the following attributes to describe forest structure: basal area, tree height, understory cover, canopy cover, and slope, in four plots at each study site. In 2000, I established two 20 x 50 m (0.1 ha) plots near each of the two most intensively surveyed stations at each site. One plot was at the beginning of the station near the first mist nets, and the other was at the end near the last mist nets. I measured the diameter at breast height (*DBH*, stem diameter at 1.3 m) of all trees with $DBH \geq 10$ cm in all plots.

With these data I estimated stand basal area. I measured the heights of the five tallest trees in each plot with a clinometer. I divided each plot into five 50 m transects spaced 5 m apart (0, 5, 10, 15, 20 m) and randomly chose one transect from the three interior ones (5, 10, or 15 m) to measure understory and canopy cover percentages. I applied the line intercept method to calculate the percentage of segments intercepted by the vegetation in the understory and a concave spherical crown densiometer for each 10 m of the transect, avoiding the borders, for calculating the amount of canopy cover. In each plot, the slope of the terrain was also calculated with a clinometer at a mean distance of 12 m.

Data Analysis

Mean relative abundance of species was estimated from 3 years (1998-2000) of data as the number of monthly individuals captured per mist netting effort for total, season, strata, and sex. The months of July through December 1997 were not included in this analysis. For the seasonal analysis, seasons were defined as the dry season, from January to April; the early rainy season, from May to August; and the late rainy season, from September to December. A *Kruskal-Wallis* test was used to evaluate differences in this index over years, across seasons, and between strata and forests for the most abundant nectarivores and frugivores (Sall and Lehman 1996). A heterogeneity G^2 goodness-of-fit test was used to determine differences in strata preference among seasons and differences in sex ratio according to season and strata.

I compared annual rainfall using G^2 goodness-of-fit test and mean monthly precipitation and T_a, $T_a$max, and $T_a$min between sites using a *t*-test. Differences in mean values of tree height, canopy cover (%), understory cover (%), basal area (m^2/ha), and slope between the two sites were determined using a *t*-test.

Results

Rainfall and Temperature

The cloud forest had a higher mean annual rainfall (n = 4 years) (Table 2-1) (t = 3.96, $df = 2$, $P < 0.001$) and higher rainfall by year than the lowlands (G^2 • 38.2, df's = 1, $P < 0.001$) (Figure 2-4). At both sites rainfall increased from 1997 to 1999, but decreased in 2000 (Figure 2-4). Both sites had similar seasonal rainfall patterns (Figure 2-5). In the lowlands, the lowest mean monthly values of rainfall (• 100 mm) were from January to April and the highest (• 250 mm) values were from May to November. In the cloud forest, the lowest mean monthly values of rainfall were from January to March and the highest were from May to November (Table 2-1). The cloud forest had two peaks in rainfall during the year: one in June and another in September. The lowland site also had peaks in June and September, but these peaks were smaller than in the cloud forest.

Mean monthly temperature, maximal temperature, and minimal temperature were lower in the cloud forest than in the lowland site (t-tests • 15.881, df's = 2, P's < 0.001) (Table 2-2). Differences between diurnal and nocturnal temperatures (ΔT_a) were greater in the dry season than in the rainy season in the lowlands and in the rainy season than in the dry season in the cloud forest, but the differences were more evident in the lowlands (Figure 2-6). In the lowlands, with the beginning of the dry season, $T_a$max tended to increase, while $T_a$min tended to decrease, whereas during the beginning of the rainy season they showed the opposite trend. In the highlands with the beginning of the dry season, both $T_a$max and $T_a$min tended to decrease, whereas with the beginning of the rainy season $T_a$max showed an increasing trend, $T_a$min tended to increase and remain stable until August, when it began to decrease.

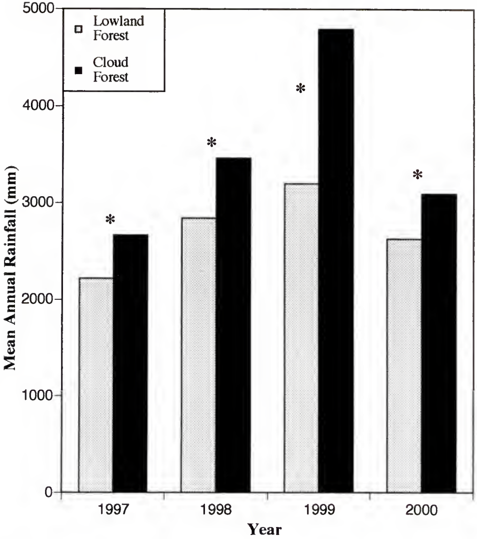


Figure 2-4. Mean annual rainfall values (mm) for a cloud forest (Fortuna 1010 m) and a lowland site (Facultad de Ciencias Agropecuarias: FCA 35 m) from 1997 to 2000. The asteriks indicate significant differences between sites using *G*test (* $P < 0.0001$).

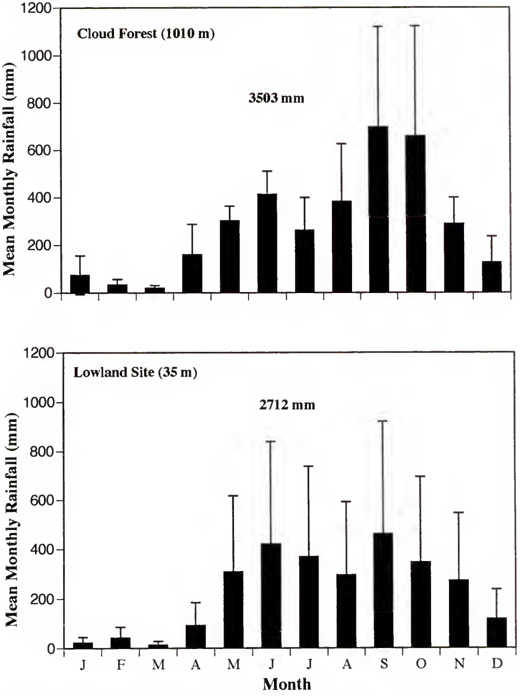


Figure 2-5. Mean (solid bars) and standard deviation of monthly rainfall in millimeters (mm) for meteorological stations in a cloud forest (Fortuna) and a lowland site (Facultad de Ciencias Agropecuarias) with the elevations expressed in meters (m). Both sites have 4 years records (1997-2000). Mean annual rainfall in millimeters (mm) is shown for cloud forest and lowland site.

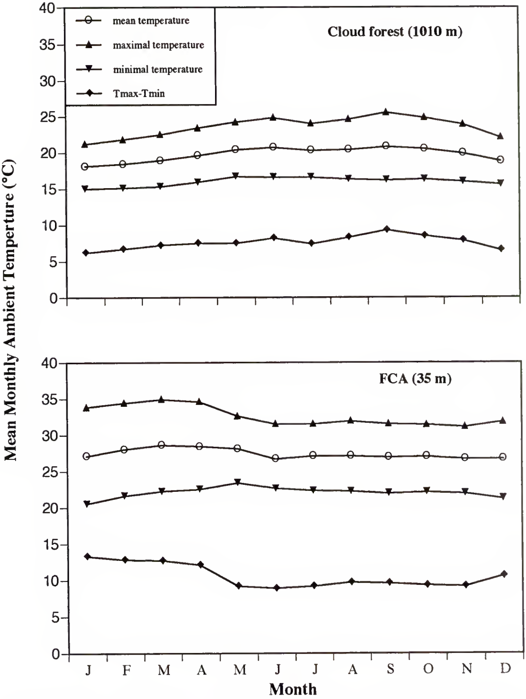


Figure 2-6. Mean monthly ambient temperature, maximal temperature, minimal temperature, and differences between maximal and minimal temperature in a cloud forest (Fortuna) and a lowland site (Facultad de Ciencias Agropecuarias: FCA). Temperature values are expressed in degrees Celsius (°C) and elevation in meters (m). Temperature records are for 4 years (1997-2000).

Table 2-1. Mean monthly and annual rainfall (mm) values (± SD) recorded in lowlands (Facultad de Ciencias Agropecuarias and cloud forest (Fortuna) meteorological stations. Rainfall records are for 4 years (1997-2000). Site elevation for lowlands was 35 m. Site elevation for cloud forest was 1010 m.

	Mean rainfal in mm (± SD)	
Month	Lowlands (35 m)	Cloud forest (1010 m)
January	22.5 (± 17.4)	74.8 (± 81.2)
February	43.6 (± 30.7)	33.6 (± 23.1)
March	17.6 (± 18.6)	19.8 (± 12.0)
April	92.2 (± 86.3)	161.0 (± 125.9)
May	308.2 (± 105.1)	301.9 (± 63.0)
June	419.5 (± 96.9)	413.8 (± 98.3)
July	369.3 (± 92.3)	262.3 (± 138.2)
August	296.1 (± 176.9)	384.1 (± 244.2)
September	460.8 (± 176.9)	698.3 (± 420.6)
October	347.4 (± 187.4)	660.3 (± 461.3)
November	273.2 (± 127.5)	290.6 (± 111.1)
December	119.0 (± 45.6)	127.7 (± 109.7)
Annual	2712.0 (± 398.6)	3503.0 (± 920.5)

Table 2-2. Mean monthly and annual ambient temperature (T_a), maximal temperature ($T_a$max), and minimal temperature ($T_a$min) (°C) recorded in the lowlands (Facultad de Ciencias Agropecuarias) (1997-2000) and in the cloud forest (Fortuna) (1997-2000). Sites elevations are reported in meter (m) and noted in parentheses.

	Mean ambient temperature in °C					
	Lowland forest (35 m)			Cloud forest (1010 m)		
Month	T_a	$T_a$max	$T_a$min	T_a	$T_a$max	$T_a$min
January	27.1	33.8	20.5	18.1	21.2	15.0
February	28.0	34.4	21.6	18.4	21.8	15.1
March	28.6	34.9	22.2	18.9	22.5	15.3
April	28.4	34.6	22.5	19.6	23.4	15.9
May	28.1	32.6	23.4	20.4	24.2	16.7
June	26.7	31.5	22.6	20.7	24.8	16.6
July	27.1	31.5	22.3	20.3	24.0	16.6
August	27.1	31.9	22.2	20.4	24.6	16.3
September	26.9	31.5	21.9	20.8	25.5	16.2
October	27.0	31.4	22.1	20.5	24.8	16.3
November	26.7	31.1	21.9	19.9	23.9	16.0
December	26.7	31.8	21.2	18.8	22.1	15.6
Annual	27.4	32.6	22.0	19.7	23.6	16.0

Forest Structure

The lowlands had a taller, more closed canopy forest with less understory cover than the cloud forest. Although the lowland forest had a lower and higher slope and basal area, respectively, than the cloud forest, these differences were not significant (Table 2-3).

Table 2-3. Study site elevations and forest structure in terms of mean value (± SD) of slope, tree height, canopy cover (%), understory cover (%), and basal area measured in a lowland forest and a cloud forest.

Parameter	Lowland forest	Cloud forest
Elevation (m)	95	1210
Slope (°)	18.7 ± 5.5	23.5 ± 4.4
Tree Height (m) **	30.6 ± 2.2	19.6 ± 3.1
Canopy Cover % *	73.1 ± 7.1	60.9 ± 6.1
Understory Cover % ***	37.2 ± 7.1	91.3 ± 3.2
Basal Area (m^2/ha)	13.8 ± 6.1	8.8 ± 2.8

* $P = 0.05$, ** $P < 0.001$, *** $P < 0.0001$

Bat Vertical Stratification

I had a total capture effort of 8977 nets-hrs. In the lowland forest the effort was 4355 nets-hrs, 1773 nets-hrs for the dry season and 2582 nets-hrs for the entire rainy season. In the cloud forest the effort was 4622 nets-hrs, 1566 for the dry season and 3056 nets-hrs for the rainy season. I captured 3857 bats belonging to 53 species at both sites, 35 species in the lowland forest and 34 species in the cloud forest (Appendix A). There was no difference in bat total abundance (1962 vs 1895, $X^2 = 1.16$, $df = 1$, $P = 0.3$) between lowland forest and cloud forest.

I found differences among bat species in overall forest strata use at both sites (Appendix A). Species belonging to the subfamilies Phyllostominae (e. g., *Tonatia silvicola*) and Carollinae (e. g., *Carollia castanea*) preferred the understory in the lowland forest, but only two cloud forest species, *Myotis nigricans* and *Sturnira mordax*, were predominantly understory bats. I also found a similar trend in preference for the canopy in small (e. g., *S. hondurensis*, *A. toltecus*, *Enchisthenes hartii*) and large (e. g., *Platyrrhinus vittatus*, *A. lituratus*) frugivorous bats in the cloud forest. The other species used both strata or their low sample size did not allow the detection of differences in the use of strata (Appendix A).

There were seasonal differences in the frequency use of strata in only two species of lowland bats, *A. phaeotis* ($G^2 = 8.9$, $df = 2$, $P = 0.01$) and *S. lilium* ($G^2 = 8.6$, $df = 2$, $P = 0.01$), with both increasing their foraging in the canopy during the late rainy season. Two lowland understory species, *T. silvicola* and *C. perspicillata* seem to use both strata equally during the rainy season. In the cloud forest two species had seasonal differences in the use of strata, *S. hondurensis* ($G^2 = 11.2$, $df = 2$, $P \bullet 0.001$) and *A. watsoni* ($G^2 = 31.8$, $df = 2$, $P \bullet 0.001$); both foraged more in the canopy during the dry season. I did not find differences in the overall proportion of males to females by strata in these two bat communities ($P > 0.05$). A detailed analysis of seasonal patterns in strata use by bats will be discussed in Chapter 4.

Bat Sex Ratio

Only two frugivorous species (*A. phaeotis*, *A. jamaicensis*) in the lowlands showed a significant departure from 50:50 in the numbers of males and females (Appendix A). Cloud forest species that showed differences in male:female ratio included a nectarivore (*H. underwoodi*) and several frugivores (e. g., *C. perspicillata*, *A. jamaicensis*, *A. lituratus*). For some species there were differences in the sex ratio between the sites (Appendix A). For example, *C. perspicillata* had an overall 1:1 sex ratio in the lowland forest, but it was female biased (1:2.5 in the cloud forest, whereas *A. jamaicensis* had more females than males (1:2.5) in the lowland, but the opposite was found (2.2:1) in the cloud forest.

There were more male *C. perspicillata* captured during the late rainy season (G^2=61. , df = 1, $P < 0.001$), more female *A. phaeotis* captured during the dry and early rainy season (G^2’s • 11.8, df s = 1, P’s < 0.001), and more female *A. jamaicensis* captured during all seasons (G^2’s > 11.8, df s = 1, $P < 0.001$) in the lowlands (Table 2-4, Figure 2-7). In cloud forest bats (Figure 2-8), more female *S. mordax* were captured from the dry season (1:1) to the late rainy season (1:2) ($G^2 = 12$, $df = 1$, $P < 0.001$), whereas *A. toltecus* switched from a sex ratio of 2.0 during the dry season to a sex ratio of 0.4 in the late rainy season (G^2’s • 4.02, df s = 1, P’s • 0.04) (Table 2-4). In the cloud forest, more females of *P. vittatus* were found in the late rainy season ($G^2 = 11.8$, $df = 1$, $P < 0.001$).

Table 2-4. Seasonal differences in the sex ratio of the most common bat species captured in a lowland forest and a cloud forest. The sex ratio was calculated from 3 years mean (1998-2000) of seasonal values of species abundance.

	Proportion of adult males to females bats			
Site / Species•	Dry season	Early rainy	Late rainy	P*
Lowland Forest				
C. perspicillata	1.0	1.2	*7.0	< 0.001
A. phaeotis	*0.5	*0.3	1.0	• 0.001
A. jamaicensis	*0.3	*0.4	*0.5	• 0.001
Cloud Forest				
S. mordax	1.0	*0.7	*0.5	• 0.04
A toltecus	*2.0	1.0	*0.7	• 0.04
P. vittatus	1.0	0.8	*0.5	< 0.001

•*C.*: *Carollia*, *A.*: *Artibeus*, *S.*: *Sturnira*, and *P.*: *Platyrrhinus*. *Likelihood ratio chi-square (G^2).

Discussion

This long-term study has demonstrated that bat capture-rates vary with forest type and season in terms of vertical stratification and sex ratio. Previous studies, addressing the vertical stratification in bats, did not sample in different seasons (e. g., Bernard 2001, Kalko and Handley 2001, Lim and Engstrom 2001, but see Bonaccorso 1979), and studies focussing on the sex ratio variation did not sample in the canopy (Fleming 1988,

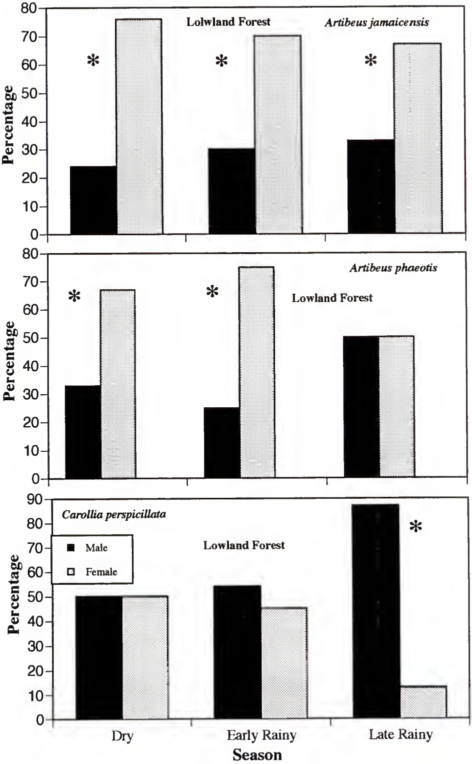


Figure 2-7. Percentage of adult male and female *Artibeus jamaicensis* (n = 752), *Artibeus phaeotis* (n = 126), and *Carollia perspcillata* (n = 222) captured across seasons in a lowland forest. An asterisk indicates a significant difference in the *G* test for that season ($P < 0.05$). Each bar represents a 3-year mean (1998-2000).

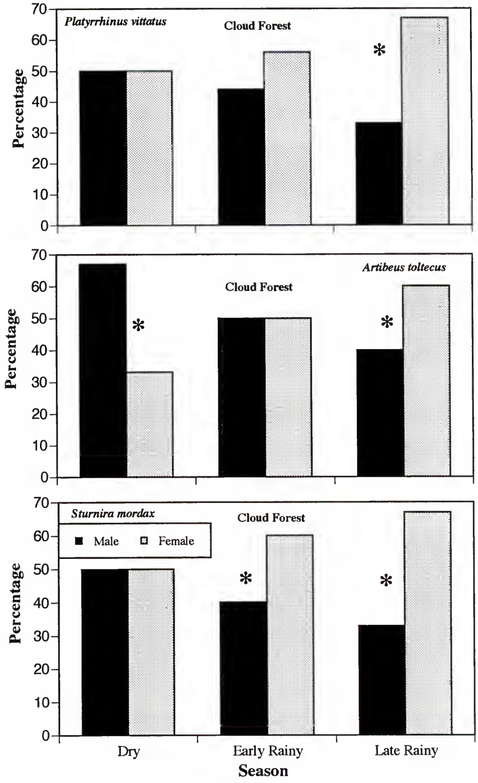


Figure 2-8. Percentages of adult males and females *Platyrrhinus vittatus* (n = 190), *Artibeus toltecus* (b) (n = 242), and *Sturnira* mordax (n = 199) captured accross seasons in a cloud forest, Panamá. An asterik indicates a significant difference in the *G* test for the season ($P < 0.05$).

Gardner *et al.* 1991, Stoner 2001). With this study, I hope to contribute to the development of a standard sampling protocol for bats, and to understanding of the bat ecology that can be applied to conservation.

Strata Use by Bats

The results indicate that lowland bats use strata differentially, whereas the cloud forest bats were mostly use the canopy. Nevertheless, in both forests the canopy was intensely used by bats, with 33 species captured in the lowland forest canopy and 29 species captured in the cloud forest canopy (Appendix A, Chapter 3).

The differences in the spatial distribution of bats may be due to differences in diet, foraging behavior, roost-site selection, or morphology (Kalko *et al.* 1996a, Fenton *et al.* 1997). Lowland species that gleaned insects (e. g., *T. silvicola*) or understory plants such as *Piper* and *Solanum* (e. g., *C. perspicillata*, *C. castanea*) were predominantly understory bats, whereas those species that feed on canopy fruits such as *Ficus* (e. g., *Artibeus* spp.) were mainly canopy bats, as in other studies (Bonaccorso 1979, Bernard 2001, Kalko and Handley 2001, Lim and Engstrom 2001). The only understory cloud forest bat was *S. mordax*, which feeds on *Solanum* and *Piper* (Dinerstein 1983). As in the lowlands, large and small cloud forest bats (e. g., *Artibeus* spp. and *P. vittatus*) that feed on canopy fruits had more captures in the canopy than in the understory; however, bats in the genus *Carollia* had also high capture rates in the canopy. *Carollia perspicillata* feeds on canopy fruits during the late rainy season on Barro Colorado Island (Bonaccorso 1979, Thies 1998). Large frugivorous bats in the cloud forest were almost exclusively using the canopy. The dense understory in the cloud forest can be the main cause of the high canopy captures of large bats. For example, *A. jamaicensis*, in the lowland forest with an open understory, had 70% of canopy use, whereas in the cloud forest, with a dense understory, this species had 89% of canopy use.

A seasonal change in the strata use by bats was found in lowland canopy frugivores: *S. lilium* and *A. phaeotis* had more captures in the canopy during the late rainy season. However, in the cloud forest, members of the same genera (*S. hondurensis*, *A. watsoni*), used the canopy during the dry season. This opposite trend in strata use by pairs of co-generic species suggests contrasting plant phenology in these sites (Heithaus *et al.* 1975, Bonaccorso and Humphrey 1984, Dinerstein 1983, 1986, Fleming 1988, 1992).

Bat Sex Ratio

Several species of bats at the two sites showed a departure from the expected 1 male:1 female adult sex ratio. In temperate bats, adult sex ratios are frequently male biased in hibernating as well as in non-hibernating species (Gaisler 1979, Keen and Hitchkock 1980). In the lowland forest, all sex ratios that differed from 1:1 (*A. phaeotis*, *A. jamaicensis*) are female biased. Previous studies in lowland bats indicate that *Phyllostomus hastatus*, *P. discolor*, and *A. jamaicensis* are female biased and that these species have harem-polygynous mating systems (McCraken and Bradbury 1981, Fleming 1988, Gardner *et al.* 1991). A study in a Costa Rica dry forest found *A. jamaicensis* with an overall sex proportion of 1:1 (Stoner 2001), but this study did not sample in the canopy. For some species, a low sample size due to captures only in the understory may limit the ability to detect a significant departure from the expected 50:50 sex ratio. *Artibeus jamaicensis* differed with forest type in the frequency use of strata.

In the cloud forest, five species were female biased and two were male biased. For example, the nectarivorous *H. underwoodi* had higher abundance of females, with only four males in the 46 individuals captured. This proportion of males to females suggests spatial segregation of sexes in *Hylonycteris*, as has been indicated for *Centurio senex* (Goodwin and Greenhall 1961, Handley 1966, Paradiso 1967). This marked difference in the proportion of males to females might not be detected if I had sampled only in the understory, because this bat used both strata equally. *Carollia perspicillata* has been reported in lowland Panamá and Costa Rica with an adult sex ratio of 1:1 (Fleming 1988, Thies 1998, Stoner 2001, this study), but this species in the cloud forest had a female-biased sex ratio. The increase in females in the cloud forest, where this species showed a migratory pattern (Chapter 4), could represent immigration of females from areas outside of my study site, as has been argued by Fleming (1988). This species is reported as rare in Monteverde cloud forest in Costa Rica (Dinerstein 1983, Timm and LaVal 2000ab), but "rareness" in *C. perspicillata* can result from its migratory behavior and canopy preference in cloud forests, and sampling only in the understory.

Artibeus jamaicensis, also with some degree of migratory behavior (Chapter 4), had a male biased sex ratio, which differed from its lowland population. Furthermore, I captured only six females in reproductive condition of 34 recorded during the 3.5-years, which may indicate that cloud forest conditions (e. g., food plants, climate) impose a nutritional/energetic constraint on females. A differential distribution of sex ratio with elevation has been demonstrated for temperate insectivore bats, which show few females at high elevation, especially in reproductive condition (Cryan *et al.* 2000).

I detected seasonal variation in the sex ratio of two lowland species. For example, although *C. perspicillata* had an overall sex ratio of 1:1, it had more males present during the late rainy season than in the dry and early rainy season. In Costa Rican dry forests this species also has a period with more males, but it occurs during the dry season or early rainy season (Fleming 1988, Stoner 2001). Three cloud forest bats had seasonal changes in sex ratio. More females of the understory bat *S. mordax* were found during the dry season, whereas more females of canopy bats (*A. toltecus* and *P. vittatus*) were captured during the late rainy season. Females of understory and canopy bats seem to differ in their seasonal nutritional and/or reproductive requirements in the cloud forest (Dinerstein 1986).

The identification of differences in the species' response to environmental variation is important for understanding maintenance of biological diversity and for the use of species as indicators of ecosystem "health". I have demonstrated that within bats, species' ecological response to environmental variability include the differential use of forest strata and changes in their adult sex ratio with season and site. Although it is clear that bats are sensitive to habitat disturbance, I recommend caution in the interpretation of results from studies examining bat sex ratio or the influence of forest disturbance on bats without considering their strata preferences.

CHAPTER 3

COMPOSITION AND STRUCTURE OF TWO PANAMANIAN BAT COMMUNITIES AT DIFFERENT ELEVATIONS

Introduction

The study of biological diversity is one of the central topics in community ecology because of its dependency on other ecological phenomena and its increasing loss in natural habitats, especially in the tropics (Huston 1994). The two components of diversity, species richness and abundance, are strongly related to the concept of species co-existence, and they represent basic measures to describe patterns of species co-existence (Tokeshi 2000). The identification of patterns and processes is directly related to the spatial and temporal scales of the study in which large scales deal with evolutionary factors, whereas medium to smaller scales deal with ecological factors (Wiens 1989, Huston 1999, Tokeshi 2000, Willis and Whittaker 2002). An analysis of diversity patterns and processes can be done only through the comparison of appropriate taxonomic (e. g., genera) or functional (e. g., guilds) groups (Huston 1999, Tokeshi 2000). A promising, but difficult, approach to describing patterns and processes of biological diversity is to study a speciose and ecologically important taxon with a wide distribution; bats are an ideal taxonomic group with which to take such an approach (Kalko 1997). New World bats are the most diverse mammals in terms of number of species (Wilson 1988, Findley 1993) and feeding habits (Janzen and Wilson 1983, Kalko 1997) in tropical communities. They play important roles as pollinators, seed dispersers, and predators of invertebrates and small vertebrates (Humphrey and Bonaccorso 1979, Findley 1993, Kalko 1998) and occupy many forest types (Humphrey and Bonaccorso 1979, Fleming 1986, Willig and Mares 1989). Therefore, the identification of ecological patterns in bat communities and factors influencing their diversity is important for the understanding and conservation of tropical forest ecosystems.

Currently, our knowledge of patterns and processes in bat communities is poor. This is due in part to the lack of standardized, long-term comparative studies, and behavioral and ecological data at the species level (Fleming 1986a, Willig 1986, Findley 1993, Kalko 1997, 1998, Stevens and Willig 1999). Previous studies have compared bat communities in terms of their biogeography, morphology, and ecology (Fleming 1986a, Findley 1993, Stevens and Willig 1999, 2000) using data collected in different years and with different methods. These sampling biases may limit the ability of these studies to detect evolutionary, biogeographic, or ecological patterns. None of these studies (e. g., Fleming *et al.* 1972, Thomas 1972, LaVal and Fitch 1977, Willig 1983) has considered differences in bat vertical distribution.

Bats show differential distribution in relation to season, elevation, habitat, and forest strata (Handley 1967, Bonaccorso 1979, Humphrey and Bonaccorso 1979, Bonaccorso and Humphrey 1984, Fleming 1991, Bernard 2001, Kalko and Handley 2001, Lim and Engstrom 2001). Furthermore, capture rates of some species show significant differences between understory and canopy nets (Kalko and Handley 2001). Considering the role of the forest canopy in plant and animal ecology is necessary when estimating species diversity and the mechanisms that underlie it (Lowman and Nadkarni 1995, DeVries *et al.* 1999).

I conducted a 3.5-year comparative study to describe the temporal and spatial patterns of bat richness and abundance in a lowland mixed forest and a cloud forest in western Panamá to understand the diversity patterns in bat communities. I examine ecological characteristics of species that correlate with distribution and abundance within and between sites and among seasons. This long–term study is the first in Panamá to examine the bat diversity outside of the Canal Area in Panamá and to sample canopy bats in a mid-elevation Neotropical cloud forest. Finally, I compare lowland and mid-elevation sites from Panamá, Central America, and South America, and discuss whether patterns previously observed in bat community studies are observed at the two Panamanian bat communities I studied.

Materials and Methods

Study Sites

This study was conducted at two sites in the province of Chiriquí, western Pacific Panamá (Chapter 2, Figure 2-1). The lowland site was Cerro Batipa (8° 20' 14.4" N and 82° 15' 13.2" W, Chapter 2, Figure 2-2), a private conservation area, with elevation ranging from 0 to 325 m. The site lies in a tropical moist forest life zone (Tosi 1969) and has a tropical climate with a prolonged dry season (McKay 2000, modified from De Martonne 1964). The mean annual ambient temperature is 27.5 ºC and annual rainfall is 2767 mm (years 1990-2000), with relatively constant precipitation from May to November, and a strong dry season from December to April (Chapter 2). The vegetation covers 600 ha of tropical evergreen, semi-deciduous, and drought-deciduous forests (Chapter 2, Valdespino and Santamaria 1999, Mueller-Dombois and Ellenberg 1974). The forest has a gradient in disturbance conditions, from mature closed canopy to highly disturbed open canopy forest patches. Some forest edges border teak (*Tectona grandis*) plantations or mangroves. The forest has a canopy height of 30 m and emergent trees of 40 m, with a closed canopy and relatively open understory (Chapter 2). The vegetation is described in detail in Valdespino and Santamaria (1999).

The cloud forest site was within the Fortuna Forest Reserve (8° 40'-8° 46'N, 82° 05'-82° 15'W, Chapter 2, Figure 2-2), where the Smithsonian Tropical Research Institute (STRI) has a field station, and is 45 km from the lowland site. The reserve ranges in elevation from 800 to 2000 m (Díaz 1996), but the study site spans an elevation range of 1000-1400 m. Fortuna has two life zones (Tosi 1969, Díaz 1996), premontane wet forest and lower wet mountain forest. It shows a montane oceanic climate (McKay 2000 based on De Martonne 1964), with mean annual ambient temperature of 19.7 ºC and rainfall of 3223 mm (years 1990-2000). The reserve comprises 19,500 ha of continuous lower mountain rainforest (Cavelier 1992, Diaz 1996), and is classified as a tropical ombrophilous cloud forest (Mueller-Dombois and Ellenberg 1974). The forest is 20-30 m in height, with an open canopy and emergent trees of 40 m, and a dense understory (90% of cover) (Cavelier 1992, Chapter 2). A detailed description of the vegetation at Fortuna is found in Mayo *et al.* (1977), Cavelier (1992), Valdespino and Santamaria (1999), and MacPherson (2000).

Bat Inventory and Monitoring

I conducted the field study from July 1997 to December 2000, except for June 1998. I sampled each bat community with mist nets for 1 to 4 nights monthly (mean = 2 nights), depending on weather. Ten sampling stations were established in the lowland forest and seven in the cloud forest. Each station was sampled for 1 to 2 nights with eight 2.5 x 12 m mist nets, using Bonaccorso's (1979) "grid" arrangement (Kalko and Handley 2001). At each station, nets were set inside the forest in parallel pairs, one at the understory level (0-3 m), the other at subcanopy/canopy level (6-15 m) and worked simultaneously in trails or natural openings in the vegetation (Figure 2-3 Chapter 2). Pairs of mist nets were separated by 20-50 m. Nets were set in the canopy using a system of ropes and plastic rings. Nets were usually opened from sunset (1800 h) to midnight (2400 h) and checked every 30-60 min.

Captured bats were placed in individual cloth bags, identified, marked, and released within 1 hour of capture. Bat species identification was based on keys for Panamanian lowland and western highland bats (C. Handley manuscripts) and a field guide of Central American mammals (Reid 1997). Only adult and subadult bats were marked. The first year of the study I used a combination of colored beads on plastic necklaces (Medellin *et al.* 2000), and afterwards used numbered metal bands on plastic (small bats) or ball-chain (large bats) necklaces (Handley *et al.* 1991). I recorded species, sex, age, reproductive condition, forearm length, body mass, hour, and location (station, net number, and strata). The use of mist nets to study bat or avian ecology has advantages and disadvantages that have discussed in detail by several authors (LaVal 1970, Fleming *et al.* 1972, Karr 1981, Kunz and Kurta 1988, see Chapter 2). My study reduced some negative biases of mist nets because it was a long-term study (3.5 y), sampled both understory and canopy, and used marked individuals.

I complemented the mist-netting survey with a bat acoustic inventory that was conducted by Sabine Müller (Universität Tübingen) under the supervision of Elisabeth Kalko (Universität Ulm/STRI). This permitted high-flying insectivorous bats that are not commonly captured with mist-nets, to be identified and included in analyses (Kalko *et al.* 1996a). The monitoring of bat ultrasound signals (echolocation) was carried out in the field using an ultrasonic microphone coupled with a bat receptor (Pettersson Ultraschall-

Detektor D 980) and recorded with a Sony Walkman WM-D6C in an audio cassette (BASF Chromdioxid Super II) during August-October 2000 at both sites with a standardized protocol (Müller 2001). By combining understory and canopy mist netting with acoustic monitoring it is possible to inventory almost the entire bat community at one site (Kalko *et al.* 1996a, Simmons and Voss 1998).

Bat Diversity Analysis

Diversity parameters were calculated for both sites and compared between habitat (lowland forest and cloud forest), height (understory and canopy), and time (year and season). The temporal factors comprise the years 1998 to 2000 and the following seasons: dry (January-April), early rainy (May-August), and late rainy (September-December). The number of species or species richness (S), taxonomic richness [genera (G) and families (F)], and taxonomic ratios (S/G, G/F) were expressed at regional and local (lowland forest and cloud forest) levels based on combined methods (mist netting, acoustic inventory, and previous inventories). The species accumulation curves, which plot the cumulative number of species discovered within a defined area as a function of the effort expended (netting nights) (Colwell and Coddington 1994, Moreno and Halffter 2000), give a preliminary estimate of species abundance. It is expected that the most abundant species are the first to be captured. Rarefaction analyses were used to compare species richness between forests and between strata (Colwell 1997). Rarefaction diversity measurements provide control for sampling differences by calculating species richness scaling all collections to the same sample size (Hulbert 1971, Heck *et al.* 1975).

Species abundance (number of individuals per species) distribution was analyzed first as the species abundance frequency distribution, in which the number of species were plotted against the $\log_2$ of abundance (Preston 1948, Magurran 1988, Hubbell 2001).

Second, it was analyzed as the dominance-diversity curve distribution (species rank-abundance) in which species were ranked according to their abundance on a $\log_{10}$-arithmetic scale (Whittaker 1965).

To describe species abundance patterns within communities, I assigned bats to an abundance category based on first captures of adults and subadults. The abundance categories are super-abundant, abundant, common, uncommon, and rare. I estimated the abundance categories using a modification of Gaston's (1994) method of the proportion of species with lowest values of abundance, with cut-off points of 20%. Although the position of the cut-off points is arbitrary, this is a simple comparative method, in which it ranked species' abundances and established a proportion of species within an abundance category.

I used Fager's "number of moves per specimen" (*NMS*), which performed best in a recent evaluation (Hubalék 2000), and Shannon-Wiener information index (*H'*), which is the most widely used measure of species diversity (Magurran 1988, Hubalék 2000) and therefore facilitates comparisons with other studies, to calculate species diversity. Fager's number and Shannon-Wiener index have maximum values of diversity around 1.0 and 3.5, respectively (Fager 1972, Magurran 1988). To obtain a measurement of a species' proportional abundance in a sample, I calculated Shannon's evenness index (*E*) (Magurran 1988). The evenness index is constrained between 0 and 1.0, the latter value representing a situation in which all species are equally abundant (Magurran 1988). Community similarity or beta (β) diversity was calculated with two measures: Sørensen index (C_s) and Sørensen quantitative index (C_N). The former measures only species presence-absence (taxonomy) and takes no account of the abundance of species, whereas the other measures both species presence-absence and abundance (function) (Magurran

1988). All equations used to calculate the α-, β-, and similarity indexes can be found in Magurran (1988) and Krebs (1989).

I used ANOVAs to evaluate differences in both lowland forest and cloud forest bat communities between strata and among season and the *Tukey-Kramer Honestly Significant Difference* (HSD) to control for *Type I* error. When the distribution of data was not normal I used the *Kruskal-Wallis* analysis of variance (Shapiro and Wilk 1965), or when the means had unequal variance I used the Welch ANOVA (Sall and Lehman 1996) to test for seasonal differences in species richness and abundance. Mean relative abundance of species was estimated from 3 years (1998-2000) of data as the number of monthly individuals captured per mist netting effort for total, seasonal, and strata. All other statistical tests are identified in the text.

Bat Guilds Analysis

To compare bat guilds, I first assigned each bat to a guild using the 10 categories proposed by Kalko *et al.* (1996a) and Schnitzler and Kalko (1998). Based on the original guild concept of Root (1967), each guild is composed of species that forage in similar habitats, in similar ways, for similar foods. Kalko *et al.* (1996a) and Schnitzler and Kalko (1998) classified guilds according to habitat, feeding mode, and diet of each species. They defined habitat with respect to the proximity of a bat to obstacles or clutter. “Uncluttered space” is the open area above the canopy or ground. “Background cluttered space” is at forest edges, in larger gaps, and in openings between canopy and sub-canopy. “Highly cluttered space” is very close to, or within, the vegetation. Bats foraging modes were classified as “gleaning” for species that take food from a surface, or “aerial” for those that capture it in the air. Bonaccorso (1979) added a vertical stratification component to the classification of bat guilds. Food habit classification refers to the main food consumed by a species. I obtained diet data from the literature (Fleming *et al.* 1972, Bonaccorso 1979, Dinerstein 1983, Humphrey *et al.* 1983, Handley *et al.* 1991, Kalko *et al.* 1996a) and personal observations.

To compare the composition and structure of bat communities I constructed two niche matrices based on the feeding guilds (as used by Kalko *et al.* 1996a) and body size (as indicated by average body mass McNab 1971). The first niche matrix described species richness by cell occupancy, whereas the second niche matrix described species identity and ecological characteristics (abundance and strata use). Body mass values were obtained from bats I caught and from the literature (Fleming *et al.* 1972, Bonaccorso 1979, Kalko *et al.* 1996a). Body size categories follow Kalko *et al.* (1996a) body mass classes: "very small"-≤10 g; "small"-11-20 g; "medium"-21-40 g; "large"-41-60 g; "very large"-61-90 g; and, "giant"-≥91 g. Other studies (LaVal and Fitch 1977, Smith and Genoways 1974, Willig 1986) have used forearm length as a measure of size because it is more commonly and accurately recorded than body mass. However, LaVal and Fitch (1977) and Lim and Engstrom (2001) have expressed reservations about the use of forearm length. Body mass represents better the ecological impact per individual in terms of resource consumption (Lim and Engstrom 2001).

To describe species abundance patterns within guilds, I assigned bats to an abundance category based on the first capture of their members (recaptures excluded). Because some species were not captured frequently enough to allow a statistical analysis, I used the percentage of captures within species by strata to describe species strata use. Bats were arbitrarily classified into three categories of forest strata use based on the number of total captures in canopy-level nets, expressed as percentage of total captures. A species was classified as a "canopy" bat if 64-100% of its captures were in canopy nets

(6-15 m), "both strata" bat with 34-63%, and "understory" bat with 1-33% of captures in canopy net. The "both strata" category may include understory bats that frequently use the canopy or canopy bats that frequently use the understory.

Results

Species and Taxonomic Richness

Mist nets were open for 8360 mist net hours (mnh) during 218 nights (lowlands 4060 mnh during 108 nights, cloud forest 4300 mnh during 110 nights). Acoustic monitoring was done for 72 hrs during 12 nights at each site (Müller 2001).

With the combined methods of mist-netting and acoustic inventory, and the inclusion of species from previous inventories in the cloud forest of Fortuna (Adames 1977, Olmos 1991), I recorded at the regional scale a total of 73 species, 43 genera, and seven families (Table 3-1, Appendix B). Taxonomic richness between both lowland and cloud forest was similar, as was the ratio of species to genera (spp/gen) relative to spatial scales and methods (Table 3-1). The ratio of genera to families (gen/fam) was also similar in ranking relative to spatial scales and method (Table 3-1).

I found no differences between forests in the species richness within bat families (*Paired t*-test, $P = 0.9$) or subfamilies (*Paired t*-test, $P = 0.7$). Phyllostomidae dominated both lowland forest (30 of 51 spp.) and cloud forest (34 of 52 spp.). The family Vespertilionidae followed in species richness at both lowland (7 spp.) and cloud (9 spp.) forest. Emballonuridae was rich in species in the lowlands (7 spp.), but not in the cloud forest (2 spp.). The other families were poor in representation in both forests. Within the Phyllostomidae family, the subfamily Stenodermatinae dominated at both lowland forest (12 spp.) and cloud forest (18 spp.), whereas some subfamilies showed opposite patterns in species richness with elevation (Figures 3-1, 3-2, Appendix B).

Table 3-1. Species and taxonomic richness, and taxonomic ratios of bats recorded in the lowland forest of Batipa and in the cloud forest of Fortuna partitioned by spatial scale and method.

	Taxonomic category			Taxonomic ratio	
Spatial scale/Method	# Species	# Genera	# Families	spp/gen◆	gen/fam▫
Regional:					
Combined*•	73	43	7	1.69	6.14
Mist-netting	53	29	4	1.83	7.25
Acoustic	23	14	4	1.64	3.5
Lowland forest:					
Combined*	51	31	6	1.64	5.17
Mist-netting	35	21	3	1.67	7.0
Acoustic	19	12	4	1.58	3.0
Cloud forest:					
Combined•	52	28	6	1.86	4.67
Mist-netting	34	20	3	1.70	6.67
Acoustic	15	9	4	1.67	2.25

* Includes visual observations in the lowlands of *Noctilio leporinus* and *N. albiventris* in a pond bordering the forest and the netting of *Vampyrodes caraccioli* in the nearby mangrove. •Includes species from two previous inventories (Adames 1977, Olmos 1991) in the cloud forest: *Saccopteryx bilineata*, *Micronycteris schmidtorum*, *Carollia castanea*, *Sturnira lilium*, *Desmodus rotundus*, *Myotis riparius*, *Thyroptera tricolor*, and *Eumops glaucinus*. ◆Proportion of number of species to number of genera. ▫ Proportion of number of genera to number of families.

For bats recorded with mist nets, species accumulation curves showed that the cloud forest accumulated species faster than the lowland forest during the first 20 netting nights. Thereafter, more species were captured in the lowlands until both curves reached similar species richness (Figure 3-3). Rarefaction analysis showed that close to 1800 captures would have been required to accumulate 34 and 33 species in the lowland forest and in the cloud forest, respectively. My actual sampling accumulated 35 species with 1965 bats and 34 species with 1896 bats in the lowland forest and in the cloud forest, respectively.

Both bat communities were numerically dominated by a few abundant and many less abundant species (Table 3-2, Figures 3-4, 3-5, Appendix B). The six most abundant species in the lowland forest (*Artibeus jamaicensis*, *C. perspicillata*, *C. castanea*, *A. phaeotis*, *A. watsoni*, and *Glossophaga soricina* in decreasing order) were mostly frugivores and accounted for about 79% of total captures (Tables 3-2, Figure 3-4, 3-5, Appendix B); the superabundant *A. jamaicensis* (n = 851) accounted for 43% of this total. The six most abundant species (*A. toltecus*, *Sturnira mordax*, *Platyrrhinus vittatus*, *S. hondurensis*, *A. lituratus*, and *C. brevicauda* in decreasing order) in the cloud forest were frugivores and accounted for about 65% of total captures. The superabundant *A. toltecus* (n = 279) accounted for 15% of the total (Tables 3-2, Figures 3-4, 3-5, Appendix B).

The number of understory and canopy species was similar in both forests (Table 3-3). For the lowlands, rarefaction analysis showed that close to 800 captures would have been required to accumulate 30 and 31 species in the understory and in the canopy, respectively. My actual sampling accumulated 31 species with 844 bats and 33 species with 1118 bats in the understory and in the canopy, respectively. For the cloud forest, rarefaction analysis showed that close to 500 bats would have been required to accumulate 26 and 23 species in the understory and in canopy, respectively. My actual sampling accumulated 28 species with 575 bats and 29 species with 1320 bats in the understory and in the canopy, respectively.

Table 3-2. Abundance categories for bat communities of lowland forest (Batipa) and cloud forest (Fortuna). Species abundance range was determined by the proportion of species method, with cut-off points of 20% (modified from Gaston 1994).

	Abundance range and number of species			
Category	Lowland forest	# Species	Cloud forest	# Species
Rare	1-5	10	1-4	14
Uncommon	6-22	15	9-24	7
Common	47-101	5	42-106	6
Abundant	119-225	4	115-224	6
Superabundant	851	1	279	1
Total	1962	35	1895	34

Table 3-3. Species richness of bats in lowland forest and cloud forest partitioned by species category and forest strata (A). Species categories: rare species are those represented by • 5 individuals, all other species are those represented by • 6 individuals, and restricted species are those species captured only in one strata level, understory or canopy. Individual abundances of bat species in these two forests partitioned by forest strata (B).

	Understory	Canopy	Total
Lowland Forest			
(A) Species richness			
rare species	8	9	10
all other species	23	24	25
total species	31	33	35
restricted species	2	4	6
(B) Individual abundance			
total individuals	* 844	* 1118	1962
Cloud Forest			
(A) Species richness			
rare species	8	9	14
all other species	20	20	20
total species	28	29	34
restricted species	5	6	11
(B) Individual abundance			
total individuals	* 575	* 1320	1895

*P<0.0001

I also found similar values in the number of species by forest strata and total between the two forests (Table 3-3). I captured significantly more individuals in the canopy than in the understory in both forests (G^{2}'s • 38.4 , *df* 's = 1, *P*'s < 0.0001). Between sites I found significantly more individuals in the understory of the lowland forest than of the cloud forest ($G^2 = 51.3$, $df = 1$, $P < 0.0001$) and more individuals in the canopy of the cloud forest than in the lowland forest ($G^2 = 16.7$, $df = 1$, $P < 0.0001$). I found no differences in total bat abundance between forest sites (1962 *vs* 1895, $G^2 = 1.2$, $df = 1$, $P = 0.3$) (Table 3-3, Chapter 2).

I found differences in the relative species abundance distribution between forests. Species abundance distribution showed a high frequency of uncommon species in the lowland forest and rare species in the cloud forest (Table 3-2, Figure 3-4). Bat species abundance distribution fits a log normal distribution in the lowland forest ($P = 0.2$, Shapiro-Wilk W-test), but not in the cloud forest ($P = 0.0007$, Shapiro-Wilk W-test) (Figures 3-4, 3-5). Species rank abundance distribution in the lowland forest showed the typical log normal distribution with one or two dominant species, whereas in the cloud forest several species were prominent (Figure 3-5).

In the lowland forest, the rank-abundance patterns of understory and canopy samples are very similar to each other and to the total sample (Figure 3-6). However, they differ in the sequence of most abundant species. Understory bats are dominated in decreasing order by *A. jamaicensis*, *C. perspicillata*, *C. castanea*, *G. soricina*, *C. brevicauda*, and *A. phaeotis*, whereas in the canopy are dominated by *A. jamaicensis*, *C. perspicillata*, *A. phaeotis*, *A. watsoni*, *Phyllostomus hastatus*, and *Sturnira lilium* (Appendix B). In the cloud forest, the rank-abundance patterns of understory and canopy samples show similar distribution (Figure 3-7). Between cloud forest strata there is a difference in the sequence of most abundant species. Understory species are represented in decreasing order by *S. mordax*, *S. hondurensis*, *C. brevicauda*, *A. toltecus*, *A. lituratus*, and *A. aztecus*, whereas in the canopy by *A. toltecus*, *P. vittatus*, *A. lituratus*, *S. hondurensis*, *A. jamaicensis*, and *A. intermedius* (Appendix B).

Species Diversity

No differences were found in bat species richness (35 vs 34 for mist netting and 51 vs 52 for combined methods) or in total abundance (1962 vs 1895, $X^2 = 1.164$, $df = 1$, $P = 0.2807$) between lowlands and cloud forest. However, lowland forest showed lower species diversity than cloud forest using both two diversity indices (*H'*, *NMS*), with significant differences for Shannon's Index (*H'*: 2.174 vs 2.667, $t = 12.974$, $df = 34$,

$P = 0.0001$) (Table 3-4). The cloud forest showed a more equal abundance distribution among species than the lowland forest (*E*: 0.756 *vs* 0.611). Between sites, at the species level there is high taxonomic (C_s for mist netting = 0.464, acoustic = 0.647, and combined = 0.582) similarity and low "functional" ($C_N = 0.172$ and $C_{MH} = 0.229$) similarity (Table 3-5). Combining sampling methods, lowlands and cloud forest have 31 species in common (Appendix B).

Table 3-4. Measures of community diversity and evenness for total and by strata bat community in lowland forest and cloud forest for bats captured with mist nets.

	Diversity and evenness indices*		
Site/Strata	NMS	H'	E
Lowland forest	0.100	2.174	0.611
Understory	0.084	2.284	0.665
Canopy	0.066	1.971	0.716
Cloud forest	0.300	2.667	0.756
Understory	0.186	2.503	0.751
Canopy	0.265	2.606	0.774

**NMS*: Fager's number of moves per specimen, *H'*: Shannon-Weiner information index, E: Shannon's evenness index.

Table 3-5. Measures of community similarity for total and by strata bat community in a lowland forest and cloud forest based on data from combined (mist netting and acoustic), mist netting, and acoustic monitoring methods.

	Community similarity indices*	
Spatial scale/Method	C_S	C_N
Regional: Lowlands *vs* Cloud forest		
Combined	0.582	-----
Mist-netting	0.464	0.172
Acoustic	0.647	-----
Lowland forest:		
Understory *vs* Canopy	0.906	00.581
Cloud forest:		
Understory *vs* Canopy	0.807	0.285

*C_S: Sorenson qualitative index, C_N: Sorenson quantitative index.

The lowland bats had a more diverse understory than the canopy, but similar evenness (Table 3-4) and higher taxonomic than functional similarity between strata (Table 3-5). The cloud forest showed similar species diversity and evenness between

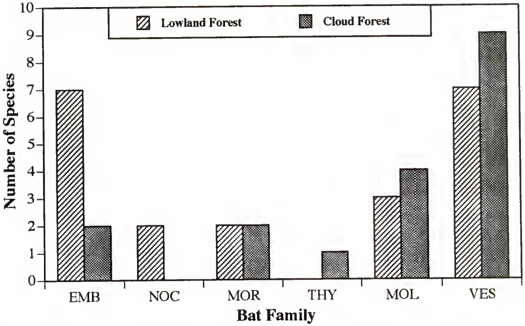


Figure 3-1. Species richness within insectivore and piscivore bat families in a lowland forest and cloud forest in Panamá. Insectivorous bats belong to the families Emballonuridae (EMB), Mormoopidae (MOR), Thyropteridae (THY), Molossidae (MOL), and Vespertilionidae (VES). Insectivorous/piscivorous bats belong to the family Noctilionidae (NOC).

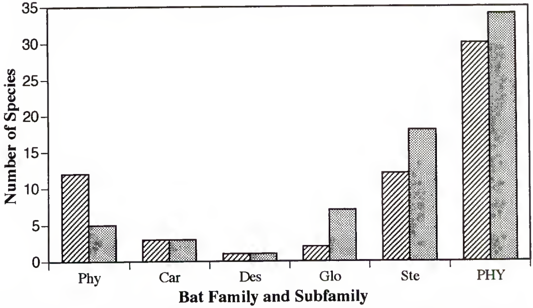


Figure 3-2. Species richness of the bat family Phyllostomidae (PHY) and its subfamilies in a lowland forest and cloud forest in Panamá. Subfamilies are the insect-omnivorous-carnivorous Phyllostominae (Phy), nectarivore Glossophaginae (Glo), and frugivore Carollinae (Ca) and Stenodermatinae (Ste).

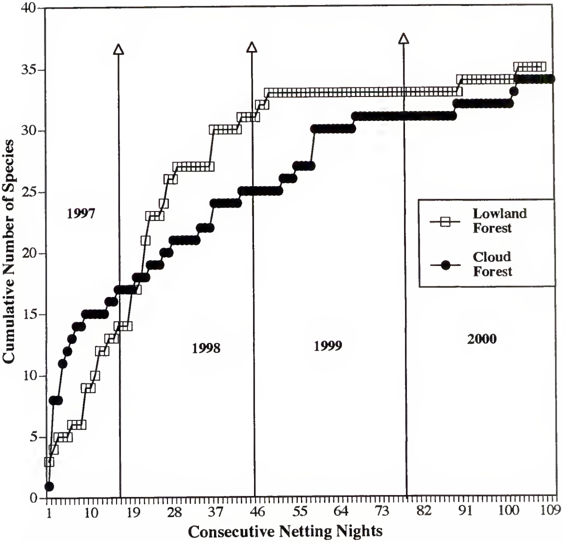


Figure 3-3. Bat species accumulation curves from two forests in Panamá at different elevations during July 1997-Dec 2000. Curves show total number of species captured partitioned by lowland forest (Batipa: 35 spp. and 108 nights) and cloud forest (Fortuna: 34 spp. and 110 nights) versus consecutive netting nights. Arrows divide netting nights in year periods.

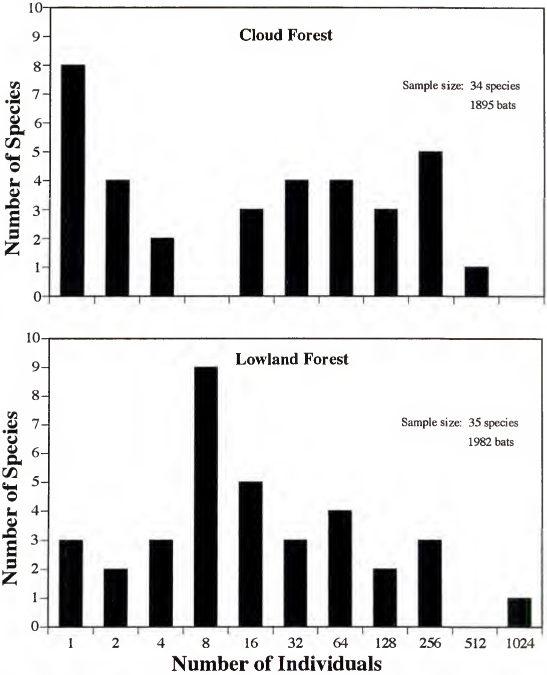


Figure 3-4. Distribution of the relative species abundance for Panamanian bats in a cloud forest (Fortuna) and a lowland forest (Batipa). Relative abundance distributions are plotted by doubling classes of abundance ($\log_2$), following the method of Preston (1948). The lowland site shows a lognormal distribution ($P = 0.2$) whereas the cloud forest the distribution is not lognormal ($P = 0.0007$) (Shapiro-Wilk W-test).

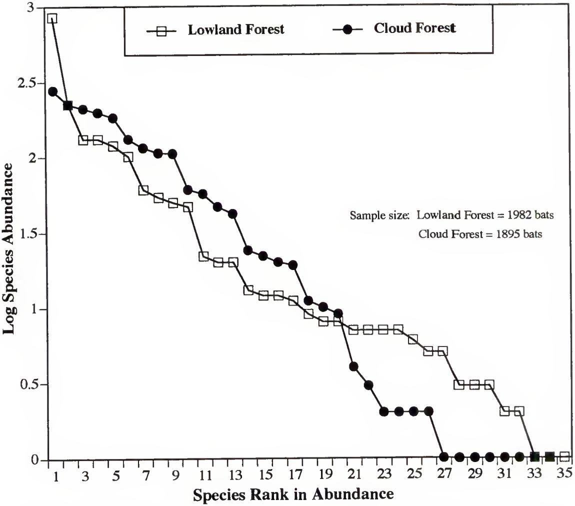


Figure 3-5. Dominance-diversity curves for bat species in two Panamanian forests at different elevations. Log_{10} of species abundance partitioning by lowland forest (Batipa: 35 species) and cloud forest (Fortuna: 34 species) bat species rank. Sample size refers to total bat abundance.

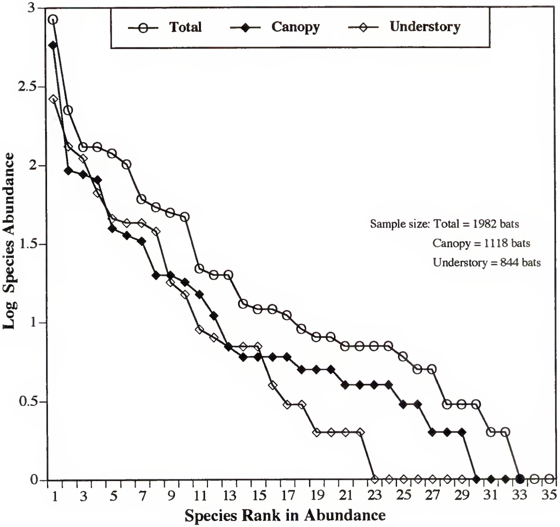


Figure 3-6. Dominance-diversity curves for the bat community in lowland forest (Batipa). Log_{10} of species abundance partitioned by total (35 species), canopy (33 species), and understory (29 species) bat species rank. Sample size refers to bat abundance for total community, canopy, and understory.

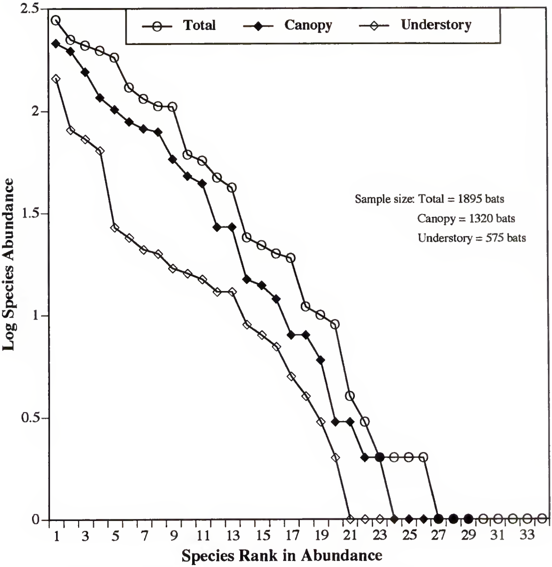


Figure 3-7. Dominance-diversity curves for the bat community in a cloud forest (Fortuna). Log_{10} of species abundance partitioned by total (34 species), canopy (29 species), and understory (28 species) bat species rank. Sample size refers to bat abundance for total community, canopy, and understory.

strata. Forest strata in the cloud forest were more taxonomically (C_s: 0.807) than functionally (C_n: 0.285) similar in bat species composition between strata (Table 3-5).

Spatial and Temporal Bat Diversity

Annual and seasonal temporal patterns of bat species richness and abundance were different between and within sites. When partitioned among years the lowland and cloud forest showed similar trends in species richness and "single species", but not with respect for abundance and "unique species" (Tables 3-6, 3-7). The trends were only significant for species richness in the lowlands ($G^2 = 5.0$, $df = 1$, $P = 0.02$) and for abundance in the cloud forest ($G^2 = 6.8$, $df = 1$, $P = 0.01$).

Table 3-6. Corrected values for annual mist netting effort◆ of bat abundance and species richness partitioned by year for the lowland forest. Single species were species represented by one individual in a year, and unique species were species not captured in any other year. Values for unique species were not corrected. Numbers in parentheses represent raw values.

Year	Abundance	# Species*	Single species	Unique species
1998	0.53 (426)	0.034 (30)	0.007 (6)	3
1999	0.55 (717)	0.022 (29)	0.003 (4)	1
2000	0.48 (707)	0.018 (27)	0.002 (3)	2
Total★	1802	35	3	6

◆Annual effort: 1998 = 876, 1999 = 1310, and 2000 = 1478 mist net-hour. ★Total are raw values that did not include bat recaptures or the count of species more than one time. *Significant differences between 1998 and 2000 ($P = 0.02$).

Monthly values of species richness, abundance, and rainfall showed high variation by year at both forests (Figures 3-8, 3-9). The partitioning among seasons showed differences in species richness and abundance patterns between forests or strata. The seasons comprise dry (January to April), early rainy (May to August), and late rainy (September to December). In the lowland forest, I found that significant variation occurred among seasons in total number of species ($F = 7.8$, $df = 11$, $P = 0.01$), understory species ($F = 9.7$, $df = 11$, $P = 0.006$), total individuals (Welch ANOVA, $F = 7.3$, $df = 2$, $P = 0.03$), understory individuals ($F = 11.4$, $df = 11$, $P = 0.003$), and canopy individuals captured ($F = 9.8$, $df = 11$, $P = 0.005$), but only a slight variation in canopy species (Welch ANOVA, $F = 5.6$, $df = 2$, $P = 0.05$). I found no differences between the understory and the canopy for either species ($F = 0.4$, $df = 11$, $P = 0.5$) or individuals ($F = 3.5$, $df = 11$, $P = 0.07$), the strata-season interactive effect was not significant in either case ($P > 0.2$) (two-way ANOVA) (Figure 3-10).

In the cloud forest, I found significant variation among seasons in total individuals ($F = 5.0$, $df = 11$, $P = 0.03$), understory individuals (Kruskal-Wallis $X^2 = 6.0$, $df = 2$, $P = 0.05$), and canopy individuals ($F = 5.9$, $df = 11$, $P = 0.02$), but not for total species ($F = 0.7$, $df = 11$, $P = 0.5$), understory species ($F = 1.4$, $df = 11$, $P = 0.3$), or canopy species ($F = 2.6$, $df = 11$, $P = 0.1$) (Figure 3-11). Also, I found significant differences between strata for species ($F = 2.4$, $P = 0.03$) and individuals ($F = 12.6$, $P = 0.002$); but strata-season interactive effect was not significant in either case ($P > 0.09$) (two-way ANOVA) (Figure 3-11).

Table 3-7. Corrected values for annual mist netting effort◆ of bat abundance and species richness partitioned by year for the cloud forest. Single species were species represented by one individual in a year, and unique species were species not captures in any other year. Values for unique species were not corrected. Numbers in parentheses represent raw values.

Year	Abundance*	# Species	Single Species	Unique Species
1998	0.31 (297)	0.024 (23)	0.005 (5)	4
1999	0.46 (698)	0.018 (27)	0.003 (4)	4
2000	0.55 (804)	0.017 (25)	0.003 (4)	3
Total★	1748	34	7	11

◆Annual effort: 1998 = 946, 1999 = 1512, and 2000 = 1460 mist net-hour. ★Total are raw values that did not include bat recaptures or the count of species more than one time. *Significant differences between 1998 and 2000 ($P = 0.01$).

In the lowland forest I captured more species (one-way ANOVA, Tukey-Kramer HSD [T-K], $P < 0.05$) and individuals (K-W $X^2 = 5.8$, $df = 2$, $P = 0.05$) during the early rainy season (May-August) than in other seasons (Figure 3-10). Both in the understory

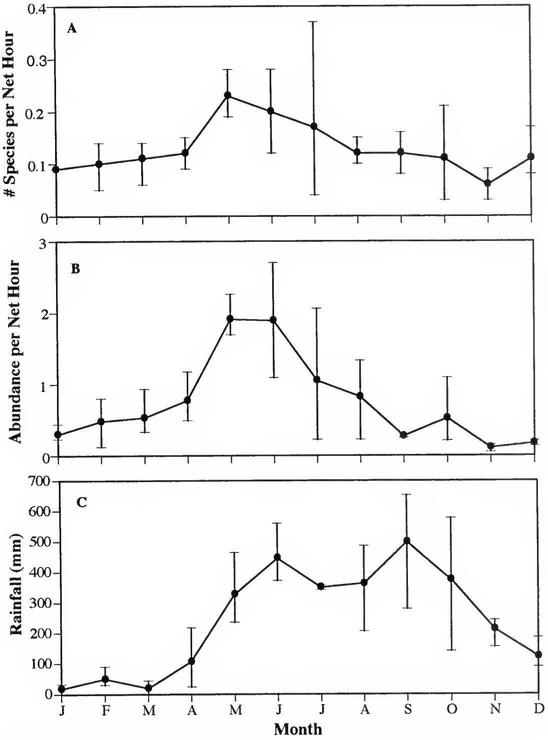


Figure 3-8. Temporal variation in the community of lowland bats from Batipa. Each monthly point represents a 3-year (1998-2000) mean with high and low values, except for June bat data which is a 2-year (1999-2000) mean. Variables are species richness (A), individual abundance (B), and rainfall (C). Species richness and individual abundance are measured as monthly species and bats captured by net hour respectively.

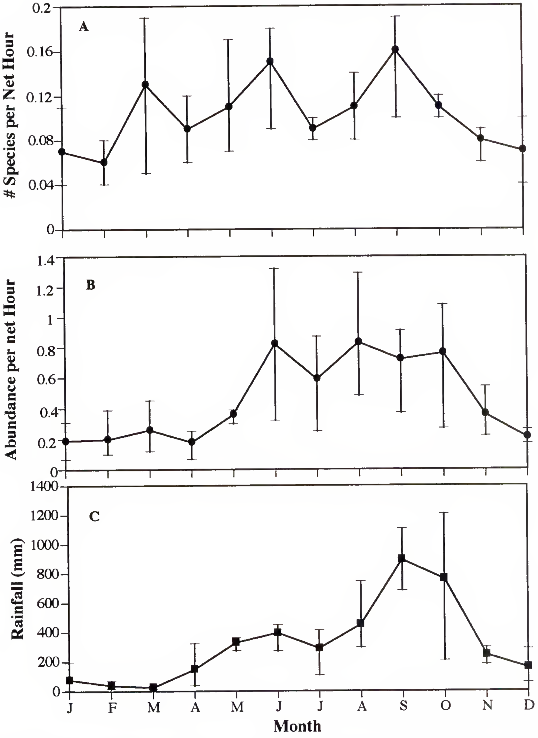


Figure 3-9. Temporal variation in the community of cloud forest bats from Fortuna. Each monthly point represents a 3-year (1998-2000) mean with high and low values, except for June bat data which is a 2-year (1999-2000) mean. Variables are species richness (A), individual abundance (B), and rainfall (C). Species richness and individual abundance are measured as monthly species and bats captured by net hour respectively.

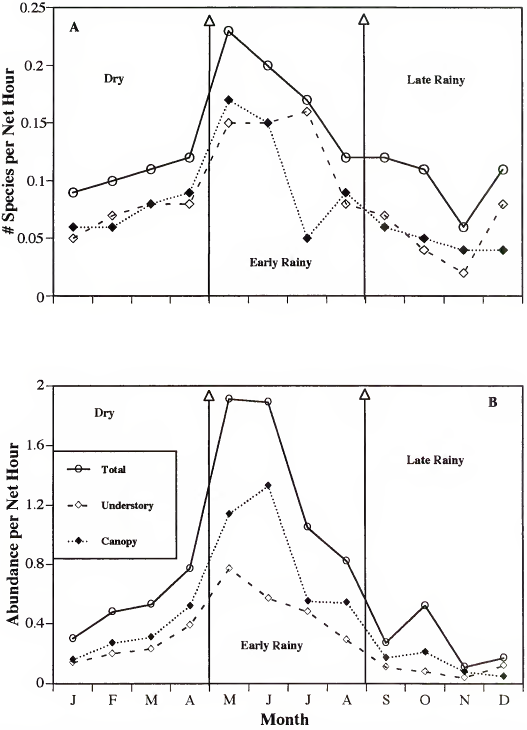


Figure 3-10. Temporal and spatial variation in the community of lowland bats from Batipa. Each monthly point represents a 3-year (1998-2000) mean, except for June bat data which is a 2-year (1999-2000) mean. Variables are for total, understory, and canopy species richness (A) and individual abundance (B) measured as monthly species and bats captured by net hour, respectively.

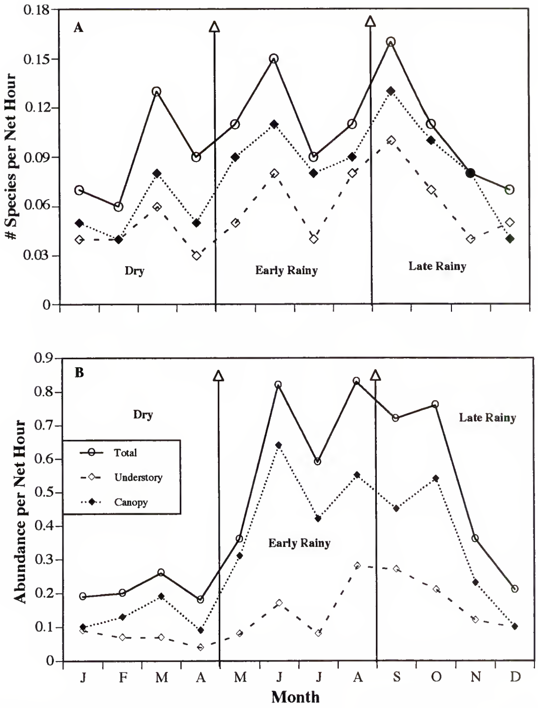


Figure 3-11. Temporal and spatial variation in the community of cloud forest bats from Fortuna. Each monthly point represents a 3-year (1998-2000) mean, except for June bat data which is a 2-year (1999-2000) mean. Variables are for total, understory, and canopy species richness (A) and individual abundance (B) measured as monthly species and bats captured by net hour respectively.

and the canopy I captured more species (understory, one-way ANOVA, T-K, $P < 0.05$; canopy, K-W $X^2 = 5.8$, $df = 2$, $P = 0.5$) and individuals (understory, Welch ANOVA, $F = 10.9$, $df = 2$, $P = 0.02$; C, K-W $X^2 = 8.8$, $df = 2$, $P = 0.01$) during the early rainy season than in other seasons (Figure 3-10). In the cloud forest there were no differences among seasons for total number of species ($F = 0.7$, $df = 11$, $P > 0.5$), understory species (one-way ANOVA, T-K, $F = 1.42$, $P > 0.05$), or canopy species (one-way ANOVA, T-K, $F = 2.64$, $P > 0.05$) captured. For total individuals (K-W $X^2 = 7.13$, $df = 2$, $P = 0.03$), understory individuals (K-W $X^2 = 6.0$, $df = 2$, $P < 0.05$), and canopy individuals (Welch ANOVA, $F = 10.6$, $df = 2$, $P = 0.02$) I captured fewer bats during the dry season (January-April) than in other seasons (Figure 3-11).

Guild Composition and Structure

Species and taxonomic richness

Bats belonged to 10 guilds in the lowland forest and seven guilds in the cloud forest. Two of the three missing guilds in the cloud forest, the ‘highly cluttered space gleaning omnivore’ and the ‘highly cluttered space gleaning carnivore’, are represented in the lowlands by members of the subfamily Phyllostominae with 3 and 1 species, respectively. The third missing guild is the lowland ‘highly cluttered space gleaning piscivore’, represented by the family Noctilionidae (1 sp.) (Tables 3-8, 3-9, Appendix B).

I found no differences in species richness by guild between these forests (Wilcoxon Signed-Rank test, $P = 0.7$). The frugivore guild was dominant in number of species at both lowland (15 spp.) and cloud forest (21 spp.), as well as the ‘background cluttered space aerial insectivore’ (lowland forest 15 spp., cloud forest 13 spp.). Next was the gleaning insectivore with more species in the lowlands (7 spp.) than in the cloud forest (4 spp.), whereas the ‘highly cluttered space gleaning nectarivore’ showed fewer species in the lowlands (3 spp.) than in the cloud forest (8 spp.). The other guilds had low species richness at both forests (Tables 3-8, 3-9). The omnivore, carnivore, and piscivore guilds were only recorded in the lowlands (see above).

Members of the family Phyllostomidae (Carolliinae and Stenodermatinae) comprise the guild of frugivore at both forests, whereas the background aerial insectivore consists of Vespertilionidae, Emballonuridae, and Mormoopidae at both forests with the addition of Noctilionidae and Thyropteridae in the lowlands and the cloud forest, respectively. In both forests, the family Phyllostomidae comprises the members of the gleaning insectivores (Phyllostominae) as well as in the nectarivores (Glossophaginae and Phyllostominae). The uncluttered aerial insectivores were members of the families Molossidae and Emballonuridae in the lowlands, but Molossidae only in the cloud forest, whereas the sanguivore of the Phyllostomidae (Desmodontinae) occurred at both forests. The highly cluttered aerial insectivore was a member of the family Mormoopidae and the omnivore, carnivore, and piscivore guilds were described above for the lowlands (Appendix B).

Body mass

Both forests showed similar species richness by body mass distribution (Wilcoxon Signed-Rank test, $P = 1.0$). In decreasing order of species richness, the body mass ranges of 11-20 g (small) and ≤10 g (very small) showed the highest values both in the lowland forest (20 and 17 spp.) and in the cloud forest (22 and 17 spp.). These ranges included members of five and four guilds, respectively; each range is dominated by the 'background cluttered space aerial insectivore' and frugivore' guilds at both forests. The range of 21-40 g (medium) showed the highest number of guilds with six at both forests (Tables 3-8, 3-9).

Niche Matrix

The cells with the most species in the lowland forest were ≤10 g 'background cluttered space aerial insectivore' (10 spp.) and 11-20 g frugivore' (9 spp.). In the cloud forest the most occupied cells were 11-20 g 'highly cluttered space gleaning frugivore' (12 spp.) and ≤10 g 'background cluttered space aerial insectivore' (8 spp.) (Tables 3-8, 3-9).

Aerial insectivores represented most of the smallest bats (≤10 g) in both forests. Within its body mass range, background cluttered aerial insectivore had more species and genera than any other aerial insectivore guild at both sites. The genera *Myotis*, *Saccopteryx*, *Peropteryx*, and *Eptesicus* had more than one species in this guild. The uncluttered and highly cluttered aerial insectivores were dominated by the genera *Molossus* and *Pteronotus*, respectively, in both forests (Tables 3-8, 3-9, Appendix B).

The guild of gleaning insectivores had more species in the smallest size class (•10 g) and the genus *Micronycteris* dominates in number of species in both forest (Tables 3-8, 3-9). At the lowland forest, the three most frequent captured smallest species were segregated by strata use (*M. minuta, M. microtis*, and *G. sylvestris*). The two similar abundant species of small size (11-20 g) were differentiated by strata, one was an understory bat (*M. hirsuta*), the other used both strata (*Mimon crenulatum*). The only species of medium size (21-40 g) was the most frequently captured gleaning insectivore, *Tonatia silvicola* an understory bat. In the cloud forest, two species (*M. microtis* and *M. schmidtorum*) were in the ≤10 g class, and one species in each of the following classes, 11-20 g class (*M. hirsuta*) and 21-40 g class (*Trachops cirrhosus*, see the omnivorous and carnivorous guilds), all represented with only one individual.

Within the omnivore guild, the two rare small size (11-20 g) species (*Lampronycterys brachyotis* and *Trinycteris nicefori*) segregated by strata use. The ≥91 g class was represented by *Phyllostomus hastatus* a common omnivore canopy species. In the lowlands, the rare carnivorous species *Chrotopterus auritus*, represented the 61-90 g class. Sometimes *Trachops* is included within this guild or in the omnivorous guild, because of its frog-eating habits (Tuttle and Ryan 1981). The piscivore guild was represented in the 41-60 g class by *Noctilio leporinus*, which was observed only in the lowlands foraging over a pond near the forest. The sanguivore guild was represented in both forests in the 21-40 g class by *Desmodus rotundus*, a common understory species.

Table 3-8. Niche matrix of guild-body mass for 51 species of bats recorded in lowland forest of Batipa, Chiriqui, Panamá with a combined mist-netting and acoustic method.

	Range of mean body mass (g)						
Guilds*	≤10	11-20	21-40	41-60	61-90	≥91	Total
1- U S / AI		3	1				4
2- B C / AI	10	4	1				15
3- H C / AI			1				1
4- H C / GI	4	2	1				7
5- H C / GO		2				1	3
6- H C / GC					1		1
7- H C / GP				1			1
8- H C / GS			1				1
9- H C / GN	2			1			3
10- H C / GF	1	9	2	2	1		15
Total	17	20	7	4	2	1	51

*Feeding mode-U S: uncluttered space, B C: background cluttered space, and H C: highly cluttered. AI: aerial insectivore, GI: gleaning insectivore, GO: gleaning omnivore, GC: gleaning carnivore, GP: gleaning piscivore, GS: gleaning sanguivore, GN: gleaning nectarivore, GF: gleaning frugivore.

The nectarivore guild in the cloud forest was more diverse in number of species and body mass classes. In the lowlands, the two smallest nectarivorous species (≤10 g) were an abundant understory species (*Glossophaga soricina*), and an uncommon bat, that used both strata (*G. commissarisi*). The large size (41-60 g) nectarivorous canopy species, *Phyllostomus discolor*, sometimes is included in the omnivore guild. In the cloud forest, three of the four smallest species had no preference for strata but differed in abundance (*Hylonycteris underwoodi* and *Glossophaga* spp.), whereas the rare *Lonchophylla mordax* preferred the canopy. The other two size classes were represented by two uncommon canopy species, *L. robusta* and *Anoura geoffroyi* (11-20 g) and by a rare canopy species *A. cultrata* (21-40 g). The 41-60 g class was represented only by one individual of *P. discolor* (Tables 3-8, 3-9, Appendix B).

Table 3-9. Niche matrix of guild-body mass for 52 species of bats recorded in cloud forest of Fortuna, Chiriquí, Panamá with a combined mist netting and acoustic method.

	Range of mean body mass (g)						
Guild*	≤10	11-20	21-40	41-60	61-90	≥91	Total
1- U S / AI	1	1	2				4
2- B C / AI	8	5					13
3- H C / AI			1				1
4- H C / GI	2	1	1				4
5- H C / GO							0
6- HC / GC							0
7- H C / GP							0
8- H C / GS			1				1
9- H C / GN	4	2	1	1			8
10- H C / GF	2	12	3	2	2		21
Total	17	21	9	3	2		52

*Feeding mode- U S: uncluttered space, B C: background cluttered, and H C: highly cluttered. AI: aerial insectivore, GI: gleaning insectivore, GO: gleaning omnivore, GC: gleaning carnivore, GP: gleaning piscivore, GS: gleaning sanguivore, GN: gleaning nectarivore, GF: gleaning frugivore.

Frugivores represented most of the small bats (11-20 g) at both forests and occupied more size classes (n = 5) than other guilds at each forest. The smallest (≤10 g) species (*Vampyressa pusilla, Ectophylla macconnelli*) represented one of the less abundance size classes at both forests. The 11-20 g class had higher diversity of species and genera among frugivore size classes at both sites. Numerically dominant were three understory abundant-common *Carollia* spp., two canopy abundant *Artibeus* spp., and the common canopy species *Sturnira lilium*. Other genera contain only one uncommon canopy species (*Uroderma bilobatum*, *Platyrrhinus helleri*, and *Vampyressa nymphaea*). Numerically dominant in the cloud forest were four small *Artibeus* spp. that differed by forest strata and by abundance. Next was *Carollia* with two of the three species that differed by strata and abundance and by *Enchisthenes hartii*, a common canopy species. The other genera contain two uncommon canopy bats (*P. helleri* and *V. nymphaea*) and two rare species (*S. lilium* and *Chiroderma trinitatum*).

In the lowlands, the medium size (21-40 g) class included less abundant canopy bats, *C. villosum* and *V. caraccioli*, the latter was captured in the nearby mangrove. In the cloud forest, two medium size abundant species differed by strata (*Sturnira* spp.) and the third species (*Centurio senex*) was a rare bat. Both bat communities had only canopy species in the 41-60 g and 61-90 g class, and these species strongly and partially differed in abundance in the lowlands (*Artibeus* spp.), and in the cloud forest (*Platyrrhinus* sp., *Artibeus* spp.), respectively (Tables 3-8, 3-9, Appendix B).

Discussion

By extending standardized understory and canopy sampling beyond the previous one-year single-community study (Bonaccorso 1979, Bonaccorso and Humphrey 1984), I have firmly established that the diversity of bat communities varies spatially and temporally. Taking its strength from long-term, rich samples of bats, and complemented with an acoustic inventory, this study represents one of the most detailed comparative descriptions of two tropical bat communities. Therefore, I believe this study offers a standard means for comparing species diversity among sites, and exploring general spatial and temporal patterns of bats in tropical forest communities.

Description of Tropical Bat Communities

The search for patterns in community composition and structure usually has been the first step in community ecology studies because they lead in turn to the formulation of hypotheses about the causes of these patterns (Begon *et al.* 1990). Only with the kind of study shown here is it possible to sample bat communities and to compare their community attributes of composition and structure (*sensu* Putz *et al.* 2000). The addition of the acoustic method permits the identification of a component of the bat community (aerial insectivores) not easy sampled with mist nets (Kalko *et al.* 1996a).

The description of bat communities in terms of their composition (e. g., species richness, species taxonomy, and abundance) and structure (e. g., guilds, body size) permits direct comparison among communities. Species richness and abundance are the first and simplest way to describe and compare bat communities. Present in this region are 63% of the 114 bat species reported for Panamá (Samudio 2002). The lowland forest and the cloud forest showed more similarities in species richness than in abundance. Bat communities from these forests had similar species richness by combined (51 *vs* 52 spp.) or by mist netting (35 *vs* 34 spp.) methods, but not for the acoustic (19 *vs* 15 spp.) method. Comparison of bat families and subfamilies represented in these forests showed similar species richness; exceptions were Emballonuridae, Phyllostominae, and Glossophaginae. Other studies have also reported that Emballonuridae and Phyllostominae decrease in species richness with elevation, but they did not show an increase with elevation for Glossophaginae (Graham 1983, Fleming 1986a, Patterson *et al.* 1996, Soriano 2000) as was seen here.

The distribution of species richness by abundance categories (rare-superabundant) was similar in the two forests, showing the typical pattern of few abundant and more less abundant species (Kalko 1998). Nevertheless, the lowland forest seems to have more uncommon species, whereas the cloud forest seems to have more rare species. The presence of more uncommon species is typical of lowland bat communities (Kalko *et al.* 1996a), but the presence of more rare species may indicate the frequent arrival of non-resident species to the community (Hubbell 2001). Total bat abundance was similar in the forests (1962 *vs* 1895), but species abundance distribution and rank abundance were different. This comparison revealed differences in the shape of these species abundance curves that previous studies of bat community had not detected. The cloud forest bat community was more evenly distributed in species abundance than the lowland bat community, and when combined with species richness, the cloud forest bat community had higher species diversity than lowland bats. These forests were more similar in their taxonomic (C_S) than in their functional (C_N) species composition.

Forest stratification in these sites had greater impact on species abundance than on species richness. With the exception of a few species, bats used both strata in the two forests, which showed similarity in species richness by strata within and between forests. Although more bats were captured in the canopy than in the understory in both forests, many more captures were made in the cloud forest canopy. Other studies have shown a similar species pattern of strata use and a high proportion of species shared between strata (Bonaccorso 1979, Brosset and Charles-Dominique 1990, Ascorra *et al.* 1996, Simmons and Voss 1998, Bernard 2001, Kalko and Handley 2001, Lim and Engstrom 2001), but not this extreme difference in abundance. If only the understory had been sampled in my study, the cloud forest would have appeared to have low bat abundance and some species would have been incorrectly categorized as uncommon-rare. A comparison of species richness and evenness between strata in both forests showed differences in the species richness of lowland forest and cloud forest. Although, both bat communities had more taxonomically than functionally similarity between strata, the differences were greater in the cloud forest.

Temporal variation in diversity within (strata) and between forests seems to be related to patterns of rainfall (Chapter 2). The annual variability in rainfall and possibly in food resources in both forests caused high monthly variability in species richness and abundance. Both forests in 1998 showed high richness in total and single species than in other years, but unique species and abundance between forests differed in trends. In the lowlands, unique species seem to decrease with time, whereas total bat abundance was the same every year; in the cloud forest unique species seem to remain constant, while abundance increased with years. Differences in abundance trends between bat communities might result from differential changes in resident species abundance and in the number of non-resident species by year (see Hubbell 2001). At particular sites some bat species may be common one year, and rare or difficult to observe in others.

Bat species richness and abundance in Neotropical lowlands tend to be highest during early rainy season, and lowest during dry and late rainy seasons (Thomas 1972, Bonaccorso 1979, Stoner 2001, this study). However, in the cloud forest, species richness was similar in all three seasons, whereas abundance was highest during both rainy seasons (Jun-Oct) and lower during the dry season. The differences in climate and plant diversity between sites (Chapter 2) may be responsible, through their influence on the availability of food and roost resources, for the differences in seasonal diversity patterns between these bat communities (Kalko *et al.* 1996a, Kalko and Handley 2001, Fenton *et al.* 2001).

The lowland monthly variability in species richness and abundance between strata reflect the general pattern of use by bats (Kalko and Handley 2001, this study). However, there was an opposite trend between the understory and canopy species richness that has not been previously reported: understory species increased from June-July, whereas canopy species simultaneously decreased. Throughout the year both strata were used equally by individuals, which suggests that these strata may have similar resource availability. The cloud forest bats showed similar monthly trends in variability, but not in number of species or individuals, with more bats captured every month in the canopy than in the understory, maybe as a respond to forest architecture and/or food availability. This study indicates that sampling only in the understory will strongly bias the results of a bat diversity study.

The classification of species from a community into meaningful groups, such as guilds, is a way to distinguish patterns in community (Root 1967, Simberloff and Dayan 1991). Bats have been classified into 10 guilds based on habitat, feeding mode, and diet (Kalko 1997, Schnitzler and Kalko 1998). This study showed the general pattern that the number of bat guilds decreases with elevation in the Neotropics (Graham 1983, Fleming 1986a, Eisenberg 1989, Patterson *et al.* 1996, Soriano 2000). There was a decrease from the ten guilds found in lowland forests (Kalko *et al.* 1996a) to seven guilds in the cloud forest. At the well-sampled Monteverde cloud forest bat community in Costa Rica, the piscivore is the only missing guild and carnivorous and omnivorous bats are rare (Timm and LaVal 2000a).

Species absence or rareness results from physical and biological factors that influence species' niche patterns (Gaston 1994), such as food and roost availability, ambient temperature, or physiological traits (McNab 1982, 2002, Findley 1993, Kalko *et al.* 1996a). In this study, piscivorous, omnivorous, and carnivorous bats are missing in the cloud forest. The absence or rarity of these guilds might result from the scarcity of foraging ground (calm waters) and prey (piscivorous *N. leporinus*), low ambient temperature and low basal metabolic rate (omnivorous *Phyllostomus hastatus*, *N. leporinus*), or large body size and food habits (carnivorous *Chrotopterus auritus* and *Vampyrum spectrum*) (McNab 1969, 1982, Kalko *et al.* 1996a, Soriano 2000).

Bat communities were similar in their species richness, taxonomic composition, and body mass distribution of guilds in spite of ecological (e. g., elevation, rainfall, ambient temperature, and vegetation, Chapter 2) differences. Neotropical bat communities are dominated in number of species by the background cluttered aerial insectivore and the frugivore guilds (Kalko *et al.* 1996a, Bernard 2001, Kalko and Handley 2001, this study), and by small (11-20 g) and very small (≤10 g) species (Fleming *et al.* 1972, LaVal and Fitch 1977, Bernard 2001, Lim and Engstrom 2001, this study). Because results from bat studies suggest that bat communities follow similar patterns in taxonomic richness, trophic categories, and body mass distribution, at least in forest ecosystems with appropriate resources available (Fleming 1986a), the question rises of how this high bat species diversity is maintained.

Maintenance of Tropical Bat Communities

The question of how so many ecologically similar species can coexist, is one central topic in bat studies (Findley 1993, Kalko 1998). Niche differentiation is a prerequisite for a stable coexistence of similar species (Volterra 1926, Lotka 1932) and under the premise that resources are a limiting factor, members of the same guild should differ in their niche requirements (Begon *et al.* 1990). Ecological separation of species resources occurs along food, habitat, and time dimensions (Giller 1984).

McNab (1971) was the first to use a two-dimensional food habit-body size niche matrix to analyze the structure of tropical bat communities. He hypothesized that only one common species should occupy each cell in the matrix; however as in this study, it has been found that some cells contain more than one common species (Fleming *et al.* 1972, LaVal and Fitch 1977, Willig 1986, Bernard 2001, Lim and Engstrom 2001). As McNab and others have suggested, information on factors such as diet, strata use, and temporal activity, are needed to understand how tropical bat communities are structured. Tropical bats have shown differentiation according to body size, habitat use, foraging strategy, or temporal activity (Bonaccorso 1979, Bonaccorso and Humphrey 1984, Kalko 1998, Kalko *et al.* 1996a).

For example, the coexistence of several species of aerial insectivorous bats in the same body mass class can be mediated through a behavioral segregation in foraging pattern (Saunders and Barclay 1992, Kalko 1995, Kalko *et al.* 1996a), or by the influence of disturbance conditions above the canopy or at the forest edge (McKenzie and Start 1989). Lowland gleaning insectivore and omnivore species with similar body mass and abundance may use forest strata differentially (e. g., small *Micronycteris* spp.) or in some cases (e.g. *M. hirsuta* and *M. crenulatum*) may also feed on different resources (Bonaccorso 1979).

The lowland and cloud forests have only one abundant small nectarivorous bat (lowland *G. soricina* and cloud forest *H. underwoodi*). This is also the case on Barro Colorado Island and Monteverde cloud forest (Dinerstein 1983, Kalko *et al.* 1996a).

However, lowland species differentiated in strata use. *Glossophaga soricina* has a lower basal metabolic rate and smaller body size than highland nectarivorous species (McNab 1969, 1982, Soriano *et al.* 2002), and this may constraint its use of cool climate habitats. The largest member of this guild was a rare species *P. discolor*, that shows highly seasonal migratory behavior or population fluctuations (Heithaus *et al.* 1975, Humphrey and Bonaccorso 1979, Kalko *et al.* 1996a).

Neotropical frugivorous bats, which show a positive correlation between their body size and the size of fruits that they consume (Heithaus *et al.* 1975, Bonaccorso 1979, Kalko *et al.* 1996b), are divided in two taxonomic-diet groups. The genera *Carollia* and *Sturnira* are considered understory bats that feed mainly in shrubs of the Piperaceae and Solanaceae (Fleming 1986b, 1988). The Stenodermatinae (except *Sturnira*) are classified as canopy bats that feed mainly on fruits from *Ficus* (Moraceae) trees (Bonaccorso 1979, Handley *et al.* 1991, Kalko *et al.* 1996b). Only lowland bats showed the general strata-taxonomic segregation with the exception of *S. lilium*, a canopy bat. Most cloud forest frugivores were canopy specialists or made use of both strata, the latter including *Carollia* and some small *Artibeus*. The only understory specialist was the medium-sized highland species *S. mordax*. These plant-bat mutualistic associations influence the ecology of bats, and act as a mechanism that allows species coexistence (Fleming 1986ab, 1988, Kalko *et al.* 1996a).

There were few very small frugivorous bats in both forests. Lowland small-sized bats were differentiated by strata use in understory (*Carollia* spp.) and canopy (stenodermatines) and by diet in *Piper-Solanum* and *Ficus* feeding bats. Among species of *Carollia*, the segregation in body size, diet, and habitat occurs at a fine scale (Fleming 1991). The largest and smallest *Carollia* were abundant: *C. perspicillata* was one of the most abundant species in the bat community, as on Barro Colorado Island (Kalko *et al.* 1996a). *Sturnira lilium*, which shows an overlap in diet and size with *Carollia* (Fleming 1986b, 1988, Willig 1986), differed in strata use from the similar in size and abundance *C. brevicauda*. In the cloud forest, the abundant *C. brevicauda* is a mid-elevation specialist, whereas the other two *Carollia* and *S. lilium* are near margins of their limits in this cloud forest. *Carollia brevicauda* is the dominant species over *C. perspicillata* at higher elevations, on the Caribbean coast of Panamá, and on Monteverde cloud forest in Costa Rica (Dinerstein 1983, Kalko *et al.* 1996a). Low ambient temperatures seem not to be a limiting factor for these species because *C. perspicillata* and *S. lilium* have high basal metabolic rate and good thermoregulatory capacity (McNab 1969, 1982), unless they show lower masses (Audet and Thomas 1997).

Among five lowland, small canopy bats, only two (*Artibeus phaeotis* and *A. watsoni*) species were abundant. These ecologically similar *Artibeus* species may coexist through temporal or habitat differentiation (see Bonaccorso and Humphrey 1984, Kalko *et al.* 1996a). Among small, cloud forest canopy bats, *A. toltecus* was the abundant species, whereas the three common bats (*A. aztecus*, *A. watsoni*, and *E. hartii*) may have strata and temporal segregation. *Artibeus phaeotis*, which used both strata, is at the margins of its altitudinal distribution at Fortuna cloud forest.

Besides vertical stratification, other ecological factors, such as food and roost availability, need to be considered in bat resource partitioning and competition (Kalko *et al.* 1996a, Fenton *et al.* 2001). Medium to very large lowland canopy bats were poorly represented in number of individuals; the exception was the superabundant *A. jamaicensis*. The reason for this is unknown, but the availability of their preferred fruit species or suitable roosts may have influenced their abundance (Morrison 1980, Bonaccorso and Humphrey 1984, Kalko *et al.* 1996b). Two cloud forest medium-sized species of *Sturnira* were similar in abundance but differentiated in strata use. All large- to very large-sized bats were canopy species with similar abundance, but none was as abundant as the highland *P. vittatus*. In this forest, maybe fruit and roost availability and climatic factors allowed these frugivorous species to coexist at similar abundance.

For some groups of bat species, niche segregation might occur at a more fine body size-resource scale, as had been demonstrated in *Carollia* spp. (Fleming 1991, Thies 1998). A clear identification of how tropical bats partition their resources and the spatial and temporal variability in bat diversity shown here needs to be considered when the conservation actions and strategies toward the protection and management of bats and their forest habitats are developed.

In agreement with previous investigations (Thomas 1972, Bonaccorso and Humphrey 1984, Kalko *et al.* 1996a, Stoner 2001), this study confirms that Neotropical bats are a highly dynamic and flexible group of animals. It also confirms the utility of standardized, long-term sampling in diverse tropical bat communities, only by doing such sampling will it be possible to make comparisons among spatial and temporal components of diversity (Kalko 1997, 1998). My results reinforce the prevalence of variation in species richness and abundance along vertical, altitudinal, and temporal scales, accentuating the significance of considering tropical bat diversity in space and time. My comparison of two bat communities revealed differences in the shapes of species abundance distributions from lowland and cloud forests that previous work on bat communities had not detected. The differences in curve shapes suggest that these forests differ in the environmental factors that influence their bat communities (see May 1975, Stenseth 1979, Ugland and Gray 1982, Hubbell 2001). Finally, this study encourages comparisons of tropical bat communities at other lowland and highland sites, and points to a means of advancing our understanding of how spatial and temporal factors may influence tropical bat diversity and in consequence how to conserve both bats and their habitats.

CHAPTER 4

DIFFERENCES IN TEMPORAL AND VERTICAL RESOURCE USE BY LOWLAND AND CLOUD FOREST PLANT-VISITING BATS IN PANAMA

Introduction

The competitive exclusion principle (Volterra 1926, Lotka 1932) implies that similar species coexist because there should be some ecological difference between them in their niches (MacArthur 1957, 1972, Hutchinson 1959). The multidimensional niche concept (Hutchinson 1957) as a resource utilization spectrum, provides a mean to understand how species relate to one another, and enhance our interpretation of community organization (Giller 1984). Similar species can separate their activities along three major categories of resource dimensions: food, habitat, and time (Giller 1984, Colinvaux 1986). Complex resource segregation is found in assemblages with many similar species (Feinsinger 1976, Emmons 1980, Karr and Freemark 1983, Brown and Kurzius 1989, Roubik 1992).

The guild concept (*sensu* Root 1967), as a group of species that exploit the same class of environmental resources in a similar way, provides a opportunity to compare activity patterns among similar species, and to answer the question of how similar species coexist (Terborgh and Robinson 1986, Kalko 1997, 1998). Comparing guilds has been successful in the study of bat communities. Early studies of the species-rich Neotropical bat communities revealed that niche space of similar-sized bats with similar food preferences is tightly packed, especially among frugivores (Fleming *et al.* 1972, LaVal and Fitch 1977, Willig 1986). Subsequently, more complete knowledge about resources and habitat requirements of species has improved the descriptions of Neotropical bat guilds (Bonaccorso 1979, Kalko 1997, Schnitzler and Kalko 1998).

Studies of sympatric bat species in the Neotropics have revealed that partitioning of food, habitat, or temporal resources (Bonaccorso and Humphrey 1984, Marinho-Fihlo 1991, Kalko 1995) promotes coexistence of morphologically, and/or ecologically, similar species. However, broad overlap in resources and habitat use within a guild has also been documented, especially within frugivorous bats (Bonaccorso 1979, Willig *et al.* 1993, Hernández-Conrique *et al.* 1997, Giannini 1999).

New World frugivorous and nectarivorous bats in the family Phyllostomidae, are the dominant species in both lowland and highland bat communities (Fleming 1986a, 1988, Kalko *et al.* 1996a, Soriano 2000, Chapter 3). They have developed a mutualistic relationship with plants as pollinators and seed dispersers, which contributes to the maintenance of the genetic diversity of plants and the regeneration processes of the forests (Faegri and van der Pijl 1966, van der Pijl 1972, Heithaus 1982). Because plant-visiting bats are a species-rich group, it is expected that they will show a combination of diet, habitat, and temporal resource partitioning. More studies have addressed differences in diet and horizontal habitat use among plant-visiting bats (reviewed by Fleming 1992, Fleming and Sosa 1994, and Kalko *et al.* 1996b) than differences in vertical stratification (Handley 1967, Bonaccorso 1979, Bernard 2001, Kalko and Handley 2001, Lim and Engstron 2001) or temporal activity (Heithaus *et al.* 1975, Bonaccorso and Humphrey 1984, Fleming 1988, Gardner *et al.* 1991, Thies 1998, Stoner 2001). Results from Bonaccorso's study (1979, Bonaccorso and Humphrey 1984) demonstrating that bat switch strata seasonally, suggest that this behavior can be widespread among bats and that it can operate as mechanism of coexistence.

This 3.5-year study investigated the extent to which nectarivorous and frugivorous bat species differentially use the forest vertical structure and temporal resource in a lowland forest and a cloud forest in Panamá. The study focuses on species from highly diverse genera: *Artibeus*, *Sturnira*, and *Carollia*. Correlation of vertical stratification with body size, and seasonal changes in the proportion of strata use were examined. Finally, the results are discussed in the context of differences in climate, vegetation, and elevation between forests and compared with findings from previous studies.

Methods

Study Sites

I conducted this study at two sites in the province of Chiriquí, western Pacific Panamá (Chapter 2, Figure 2-1). The lowland site is Cerro Batipa (8° 20' 14.4" N and 82° 15' 13.2" W, Chapter 2, Figure 2-2), a private conservation area, with an elevation ranging from 0 to 325 m. Batipa has an elevation range of 0-325 m. The site lies in a tropical moist forest life zone (Tosi 1969) and has a tropical climate with a prolonged dry season (McKay 2000). The mean annual ambient temperature is 27.2 ºC and annual rainfall is 2768 mm (years 1990-2000), with a rainy season from May to November and a strong dry season from December to April (Chapter 2). The vegetation covers 600 ha of tropical evergreen forest, semi-deciduous forest, and dry forest (Valdespino and Santamaria 1999). The forest canopy has a height of 30 m and emergent trees of 40 m with a closed canopy and relatively open understory (Chapter 2). The vegetation is described in details in Chapter 2 and in Valdespino and Santamaria (1999).

The cloud forest site is within Fortuna Forest Reserve (8° 40' and 8° 46' N and 82° 05' and 82° 15' W, Chapter 2, Figure 2-2), where the Smithsonian Tropical Research

Institute (STRI) has a field station and is 40 km from the lowland site. The reserve has ranges in elevation from 800-2000 m (Díaz 1996), but the study site spans an elevation of 1000-1400 m. (Díaz 1996). Fortuna has two life zones (Tosi 1969, Díaz 1996): premontane wet forest and lower wet mountain forest. It shows a mountain oceanic climate (McKay 2000), with mean annual ambient temperature of 19.7 ºC and annual rainfall of 3,233 mm (years 1990-2000). The reserve comprises 19,500 ha of continuous lower mountain rainforest (Cavelier 1992, Díaz 1996), classified as a tropical ombrophilous cloud forest (Mueller-Dombois and Ellenberg 1974). The forest canopy is 20-30 m in height with an open canopy and emergent trees of 40 m, and a dense understory (Cavelier 1992, Chapter 2). Detailed description of the vegetation in Fortuna is found in Mayo *et al.* (1977), Cavelier (1992), Valdespino and Santamaria (1999), MacPherson 2000, and Chapter 2.

Bat Mist Netting

Bats were captured from July 1997 to December 2000, except for June 1998, when it was not possible to visit the sites. I sampled each bat community with mist nets for 1 to 4 nights each month, depending of the weather conditions. Ten sampling stations were established in the lowlands and seven in the cloud forest. Each station was sampled for 1 to 2 nights with eight 2.5 x 12 m mist nets using Bonaccorso's (1979) "grid" arrangement (Kalko and Handley 2001). Nets were set in pairs at 20-50 m intervals, with one of each pair set at 0-3 m (understory) and the other at 6-15 m (subcanopy/canopy) in trails or natural openings within the vegetation (Figure 2-3 Chapter 2). Nets were opened usually from sunset (1800 h) to midnight (2400 h) and checked every 30-60 min. Total sampling involved 8360 mist net hours (mnh) during 218 nights (lowlands 4060 mnh during 108 nights, cloud forest 4300 mnh during 110 nights).

Captured bats were placed in individual cloth bags, identified, marked, and released within one hour of capture. Bat species identification was based on keys for Panamanian lowland and western highland bats (C. Handley manuscripts) and a field guide of Central American mammals (Reid 1997). Only adult and subadult bats were marked. I recorded species, sex, age, reproductive condition, forearm length, body mass, hour, and location (station, net number, and strata). The use of mist nets to study bat or avian ecology has advantages and disadvantages that have discussed in detail by several authors (LaVal 1970, Fleming *et al.* 1972, Karr 1981, Kunz and Kurta 1988, Chapter 2).

Temporal and Vertical Abundance Analysis

To compare bat species abundance by strata, season, and month, I estimated a three year-mean (1998-2000) monthly species abundance, except for June, which is a 2 year-mean (1999-2000). Values for abundance were standardized by divided the monthly abundance between the monthly effort (mist net-hour). I used ANOVA to evaluate differences among monthly mean abundance of season (the average of the four months by season) within each species and the *Tukey-Kramer Honestly Significant Difference* (HSD) to control for *Type I* error. When the distribution of data was not normal, I used the *Kruskal-Wallis* analysis of variance (Shapiro and Wilk 1965), or when the means had unequal variance, I used the Welch ANOVA (Sall and Lehman 1996). Seasons were divided into dry season (January to April), early rainy season (May to August), and late rainy season (September to December).

To compare distribution of understory and canopy captures, I calculated the number of individuals captured by species in a stratum during the whole study, including the recaptures in different months. Differences in the species abundance distribution between understory and canopy were tested using a G^2 goodness-of-fit test. To examine the relationship between strata preference and body size, I used the number of canopy captures, expressed as a percentage of the total species captures, and the mean body mass. I tested with ANOVA the relationship between strata use and body size for a possible correlation of guilds: nectarivores, frugivores, *Piper-Solanum* bats, large and small fig-eating bats; and genera: *Carollia*, large and small *Artibeus*, categories (Sall and Lehman 1996). To compare seasonal differences vertical stratification among species, I used a G^2 to test for the species seasonal changes in the mean seasonal proportion (%) use of strata.

Results

Species Temporal Abundance

A total of 3627 individuals belonging to 32 species of plant-visiting bats were captured from the 3857 individuals and 53 species recorded during this study (Chapter 3). They represented 51 and 79% of the total species captured and 90 and 98% of total bat abundance recorded in lowland forest and cloud forest, respectively (Chapter 3). The cloud forest had equal or more species of plant-visiting bats in the two guilds (Appendix 2, Chapter 3).

Species abundance in nectarivorous and frugivorous bats varied over time. Most species of lowland and cloud forest plant-visiting bats had their peaks in abundance during the early rainy season or during the late rainy season (Figures 4-1, 4-2). The lowland and cloud forest species of nectarivorous bats had similar seasonal trends in abundance. Both lowland *G. soricina* (Welch ANOVA, $F = 3.31$, $df = 2$, $P = 0.11$) and cloud forest *Hylonycteris underwoodi* (one way ANOVA, Tukey-Kramer HSD [T-K], $P > 0.05$) had similar abundance among seasons. *Glossophaga* had a peak in May and was mostly absent during the late rainy season (Figure 4-1). The four lowland *Piper-*

Solanum bats differed in their seasonal abundance. On one hand, both abundant species, *Carollia perspicillata* (Wilcoxon/Kruskal-Wallis [WK-W] $X^2 = 7.54$, $df = 2$, $P = 0.02$) and *C. castanea* (WK-W $X^2 = 8.25$, $df = 2$, $P = 0.02$), had higher capture rates during the early rainy season with peaks in June and July, respectively. On the other hand both less abundant species, *Carollia brevicauda* (one way ANOVA, T-K HSD, $P > 0.05$) and *Sturnira lilium* (WK-W $X^2 = 3.14$, $df = 2$, $P = 0.2$), had similar abundance among seasons with no peaks (Figure 4-1).

The two abundant small lowland fig-eating bats, *Artibeus phaeotis* (TK HSD, $P > 0.05$) and *A. watsoni* (WK-W $X^2 = 1.25$, $df = 2$, $P = 0.5$), did not differ in abundance among seasons. I captured more individuals of the superabundant large fig-eating bat *A. jamaicensis* during the early rainy season (Welch ANOVA $F = 12.47$, $df = 2$, $P = 0.01$) with a peak in May (Figure 4-2).

Among cloud forest *Piper-Solanum* bats, I captured more *S. mordax* during the late rainy season than other seasons (Welch ANOVA, $F = 7.64$, $df = 2$, $P = 0.04$), especially in September. Within *S. hondurensis* (WK-W $X^2 = 3.72$, $df = 2$, $P = 0.15$) and *C. brevicauda* (WK-W $X^2 = 5.2$, $df = 2$, $P = 0.07$), seasonal captures did not vary significantly, but the former had two peaks in abundance (June and October) and the latter more individuals from August-November. *Carollia perspicillata* was only present in the cloud forest from August-October with its peak in August (Figure 4-1).

Four species of small cloud forest fig-eating bats, *A. toltecus* (T-K HSD, $P > 0.05$), *A. aztecus* (WK-W $X^2 = 3.1$, $df = 2$, $P = 0.2$), *A. watsoni* (TK HSD, $P > 0.05$), and *Enchisthenes hartii* (WK-W $X^2 = 4.0$, $df = 2$, $P = 0.14$) did not vary their abundance with seasons. They had peaks in abundance on March, June, and August for *A. toltecus*, on October for *A. aztecus*; and a modest peak on May for *E. hartii*, whereas *A. watsoni* had frequent captures from June-October. *Artibeus phaeotis* was mainly present in the cloud forest during the late rainy season (Figure 4-2).

For the large cloud forest fig-eating bats, I captured more individuals of *Platyrrhinus vittatus* during the entire rainy season than the dry season (WK-W $X^2 = 7.5$, $df = 2$, $P = 0.02$), whereas I captured more *A. lituratus* during the early rainy season (WK-W $X^2 = 6.78$, $df = 2$, $P = 0.04$). The other two large frugivorous bats, *A. jamaicensis* (WK-W $X^2 = 4.98$, $df = 2$, $P = 0.08$) and *A. intermedius* (WK-W $X^2 = 4.15$, $df = 2$, $P = 0.12$), did not vary in abundance among seasons. The peaks in abundance for *Platyrrhinus vittatus* was on June and October, for *A. lituratus* from June-August, for *A. jamaicensis* on June, and for *A. intermedius* on July (Figure 4-2).

Bats Vertical Stratification

Lowland plant-visiting bats clearly differentiated in their preference for a forest stratum (Chapters 2, 3, Appendix B). The lowland nectarivorous bat and three species of *Carollia* were captured more frequently in the understory than in the canopy (G^2's • 7.3, df's = 1, P's • 0.007), whereas fig-eating bats were captured more in the canopy than in the understory (G^2's • 19.5, df's = 1, $P < 0.0001$). Some species of fig-eating bats showed no stratum preference, but they had a small sample size (n • 8 individuals). Cloud forest plant-visiting bats used more frequently the canopy or both strata, with the exception of *S. mordax*, which was an understory bat ($G^2 = 23.8$, $df = 1$, $P < 0.0001$).

Species of bats in both of these forests changed patterns of strata use with elevation (species sample size • 5). Canopy captures, expressed as percentage, of nectar- and *Piper*-eating bats (*G. soricina*, *C. brevicauda*, and *C. perspicillata*), and large fig-eating *Artibeus* (*A. jamaicensis* and *A. intermedius*) were higher in the cloud forest than in the lowlands (*paired t-Test*, $t = 2.6$, $P = 0.02$, Appendix B). For small fig-eating bats (*A.*

phaeotis, *A. watsoni*, and *V. pusilla*), canopy captures were slightly less in the cloud forest than in the lowlands (*paired t-Test*, $t = -3.000$, $P = 0.048$), except for *V. nymphaea*, which had higher canopy captures in the cloud forest (75%) than in the lowlands (62%) (Appendices A, B).

I found a significant inverse correlation between log body mass and frequency (%) of canopy use among lowland small fig-eating bats, genera *Artibeus* (2 spp.) and *Vampyressa* (2 spp.) ($r = -0.98$, $P = 0.024$) (Figures 4-3, 4-4, 4-5, Appendix B). Cloud forest fig-eating bats showed a direct correlation ($r = 0.67$, $P = 0.013$). After, the analysis was extended to groups within fig-eating bats, the small fig-eating bats showed a correlation between log body mass and strata use ($r = 0.83$, $P = 0.005$). When small fig-eating bats were subdivided in two taxonomic groups, only the group of small "*Artibeus*" (including *Enchisthenes*) showed a direct correlation ($r = 0.98$, $P = 0.004$). The other categories: nectarivores, *Piper-Solanum* bats, large fig-eating bats (*Artibeus* and *Platyrrhinus*), other small stenodermatines, and genus *Carollia*, showed no significant correlation ($P > 0.05$).

Bats Vertical Stratification by Season

Some species of plant-visiting bats seasonally switched their foraging activity from one stratum to another, estimated as a seasonal change in the proportion of strata use (Tables 4-1, 4-2, Figures 4-6, 4-7, 4-8, 4-9, 4-10, 4-11, Appendix B). The lowland *G. soricina* used the understory at the same frequency during the entire year ($G^2 = 0.04$, $df = 2$, $P = 0.98$), whereas the cloud forest *H. underwoodi* progressively increased its canopy activity over the year ($G^2 = 5.98$, $df = 2$, $P = 0.05$). All lowland species of *Carollia* maintained their understory foraging behavior, but *C. perspicillata* used equally both strata during the rainy season, especially during the early rainy season ($G^2 \bullet 2.52$,

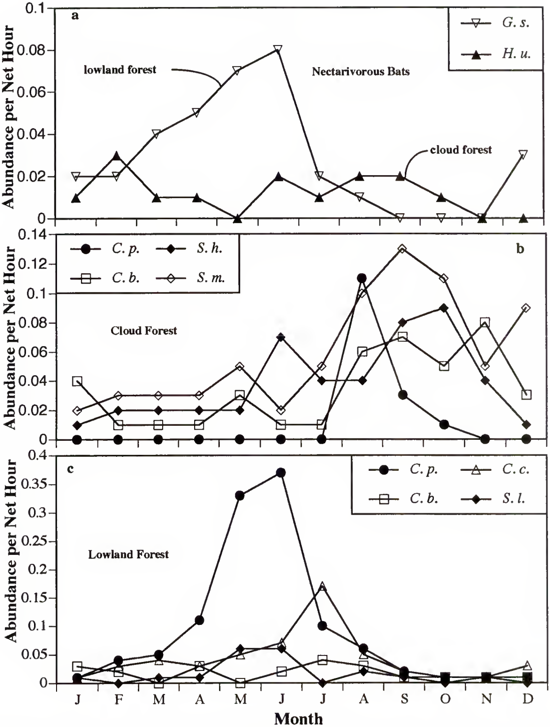


Figure 4-1. Temporal variation in species abundance (measured as monthly bats captured per net hour) of lowland and cloud forest nectarivorous (a) and cloud forest (b) and lowland (c) *Piper-Solanum* frugivorous bats. Each monthly point represents a 3-year (1998-2000) mean, except for June and cloud forest *C. p.*, which are a 2-year (1999-2000) mean. Species are *Glossophaga soricina* (*G. s.*), *Hylonycteris underwoodi* (*H. u.*), *Carollia castanea* (*C. c.*), *Carollia brevicauda* (*C. b.*), *Carollia perspicillata* (*C. p.*), *Sturnira lilium* (*S. l.*), *Sturnira hondurensis* (*S. h.*), and *Sturnira mordax* (*S. m.*).

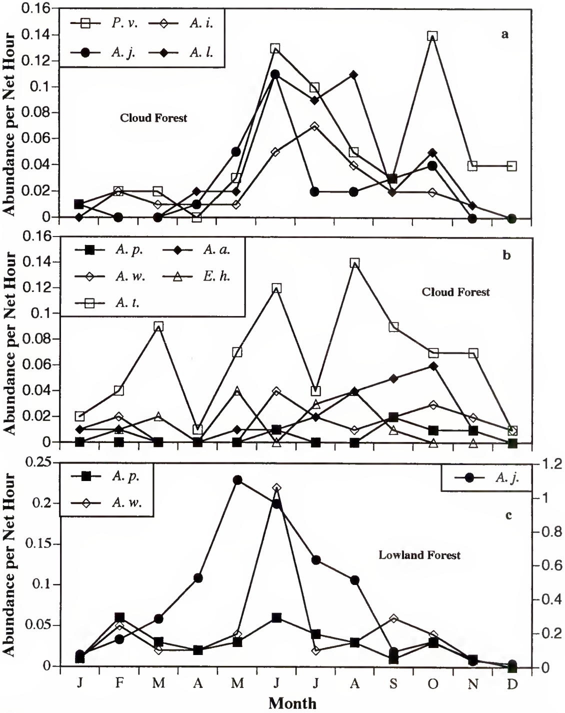


Figure 4-2. Temporal variation in species abundance (measured as monthly bats captured per net hour) of cloud forest (a) large and (b) small fig-eating bats, and (c) lowland fig-eating bats. Each monthly point represents a 3-year (1998-2000) mean, except for June bat data which is a 2-year (1999-2000) mean. Species are *Platyrrhinus vittatus* (*P. v.*), *Artibeus jamaicensis* (*A. j.*, scale at right), *Artibeus intermedius* (*A. i.*), *Artibeus lituratus* (*A. l.*), *Artibeus phaeotis* (*A. p.*), *Artibeus watsoni* (*A. w.*), *Artibeus toltecus* (*A. t.*), *Artibeus aztecus* (*A. a.*), and *Enchisthenes hartii* (*E. h.*).

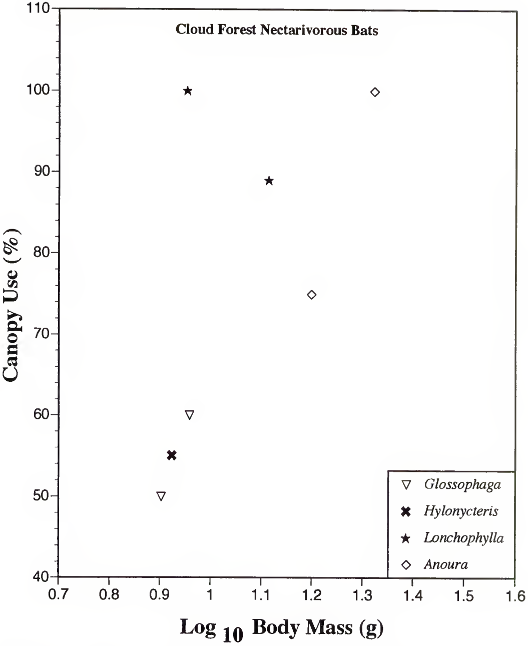


Figure 4-3. Distribution of $\log_{10}$ body massesin greams (g) of nectarivorous bats by percentage of canopy use (captures) in the cloud forest. Species are *Glossophaga commissarisi*, *Glossophaga soricina*, *Hylonycteris underwoodi*, *Lonchophylla mordax*, *Lonchophylla robusta*, *Anoura geoffroyi*, and *Anoura cultrata*.

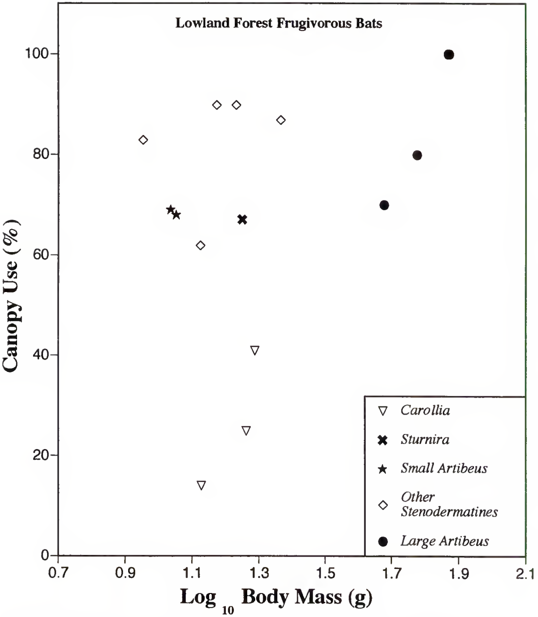


Figure 4-4. Distribution of $\log_{10}$ of body mass in grams (g) of frugivorous bats by percentage of canopy use (captures) in the lowland forest. Species are *Carollia*: *C. castanea*, *C. brevicauda*, *C. perspicillata*; *Sturnira*: *S. lilium*; small *Artibeus*: *A. phaeotis*, *A. watsoni*; Large *Artibeus*: *A. jamicensis*, *A. intermedius*, *A. lituratus*; and other stenodermatines: *Vampyressa pusilla*, *Vampyressa nymphaea*, *Platyrrhinus helleri*, *Uroderma bilobatum.*, and *Chiroderma villosum*.

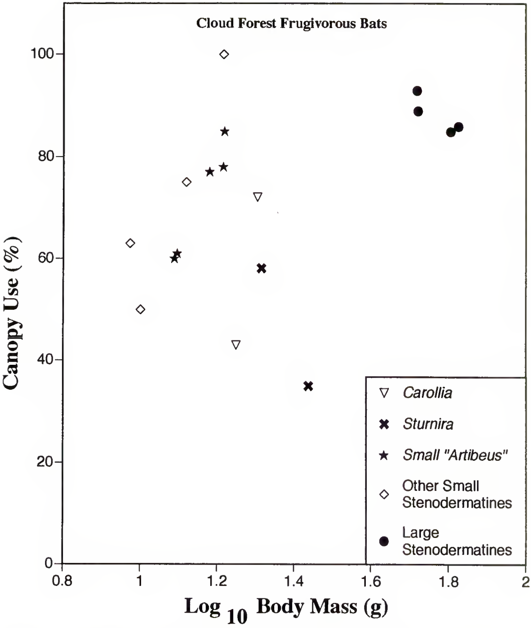


Figure 4-5. Distribution of $\log_{10}$ of body mass in grams (g) of frugivorous bats by percentage of canopy use (captures) in the cloud forest at Fortuna. Species are *Carollia*: *C. brevicauda* and *C. perspicillata*, *Sturnira*: *S. hondurensis* and *S. mordax*, small "*Artibeus*": *A. phaeotis*, *A. watsoni*, *A. toltecus*, *A. aztecus*, and *Enchisthenes hartii;* other small stenodermatines: *Ectophylla macconnelli*, *Vampyressa pusilla*, *Vampyressa nymphaea*, and *Platyrrhinus helleri;* and large stenodermatines: *Platyrrhinus vittatus*, *Artibeus jamicensis*, *A. intermedius*, and *A. lituratus*.

df = 2, P • 0.28). Canopy captures of *Sturnira lilium* increased during the late rainy season (G^2 = 8.6, *df* = 2, *P* = 0.01). Lowland small *Artibeus* maintained their canopy behavior during the year although *A. phaeotis* increased its activity in the canopy during the late rainy season (G^2 = 8.9, *df* = 2, *P* = 0.01). All lowland large frugivorous bats, *Artibeus*, were captured mainly in the canopy but only the large sample size of *A. jamaicensis* allowed an analysis. *Artibeus jamaicensis* did not change the proportion of strata use with season (G^2 = 1.42, *df* = 2, *P* = 0.5).

Among cloud forest *Piper-Solanum* bats, the abundant *S. mordax* (G^2 = 1.4, *df* = 2, *P* = 0.5) and the less abundant *C. brevicauda* (G^2 = 4.3, *df* =2, *P* = 0.1) prominently flew in the understory, although, the latter used both strata equally during the late rainy season. The other abundant species, *S. hondurensis*, was captured more frequently in the canopy, especially during the dry season (G^2 = 11.2, *df* = 2, *P* = 0.004) and the rare rainy season visitant, *C. perspicillata* used more the canopy than the understory (*P* = 0.0004, Chapter 2) (Table 4-1, Figure 4-8).

Table 4-1. Proportion of canopy to understory bat captures by season for lowland nectarivorous and frugivorous bats. Proportions were calculated from 3 year-mean (1998-2000) seasonal values of species abundance•.

	Proportion of canopy to understory bat captures			
Species•	Dry season	Early rainy	Late rainy	P*
G. soricina	0.5	0.5	0.5	n. s.
C. perspicillata	0.5	0.8	0.7	n. s.
C. castanea	0.1	0.1	0.1	n. s.
C. brevicauda	0.4	0.3	0.2	n. s.
S. lilium	6.0	2.3	10	0.01
A. watsoni	1.7	2.5	4.3	n. s.
A. phaeotis	3.1	2.7	13.0	0.01
A. jamaicensis	1.8	2.6	6.0	n. s.

•Only those species with sample size •40 individuals. •*G.*: *Glossophaga*, *C.*: *Carollia*, *S.*: *Sturnira*, and *A.*: *Artibeus*. *Likelihood ratio chi-square (G^2).

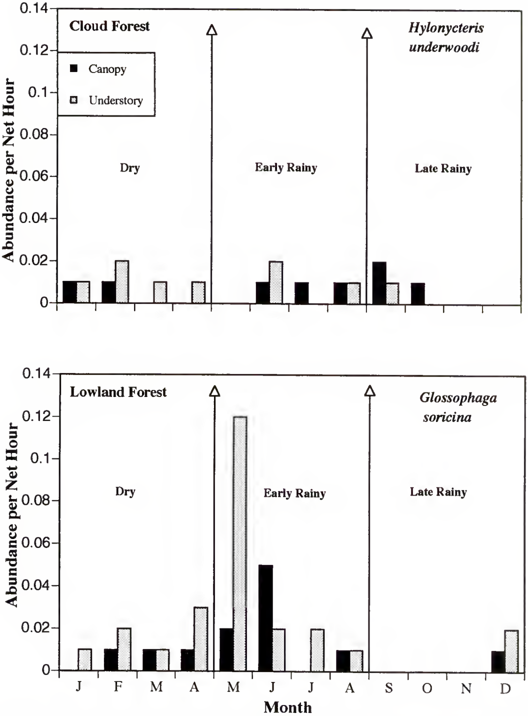


Figure 4-6. Temporal and vertical activity of a lowland (*Glossophaga soricina*) and a cloud forest (*Hylonycteris underwoodi*) nectarivorous bat. Species abundance measured as monthly bats captured per net hour in the forest understory and canopy. Each monthly bar represents a 3-year (1998-2000) mean, except for June which is a 2-year (1999-2000) mean.

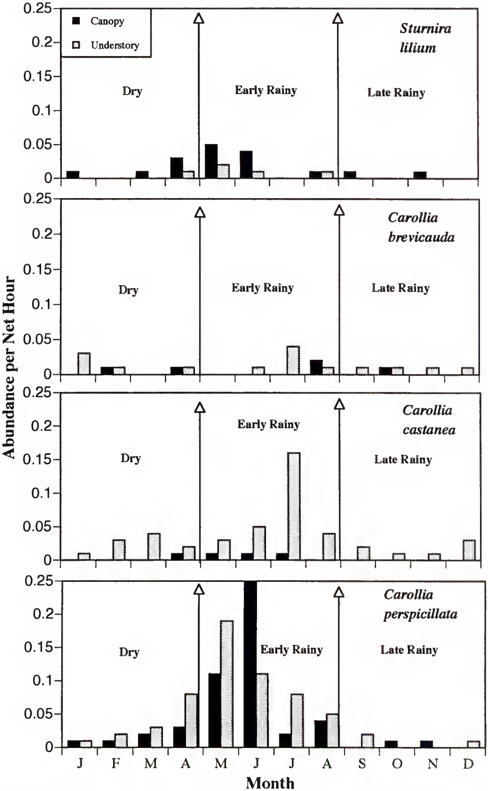


Figure 4-7. Temporal and vertical differentiation of lowland *Piper-Solanum* bats, genera *Carollia* and *Sturnira*. Species abundance measured as monthly bats captured per net hour in the forest understory and canopy. Each monthly point represents a 3-year (1998-2000) mean, except for June which is a 2-year (1999-2000) mean.

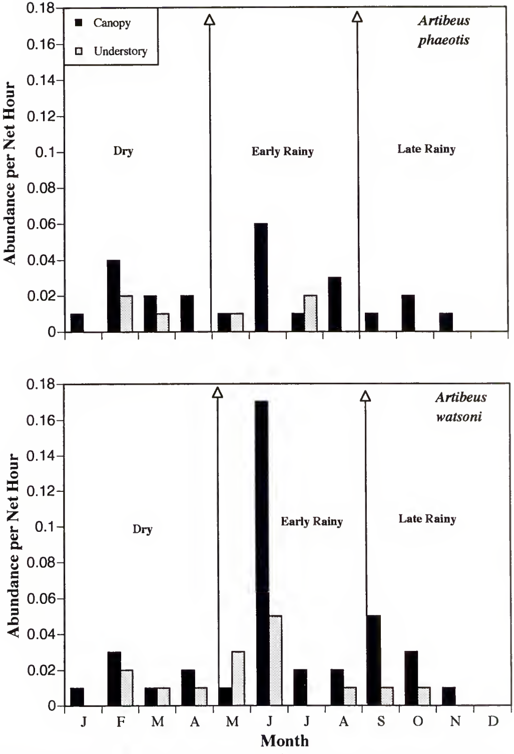


Figure 4-8. Temporal and vertical differentiation of lowland small fig-eating bats, genus *Artibeus*. Species abundance measured as monthly bats captured per net hour in the forest understory and canopy. Each monthly bar represents a 3-year (1998-2000) mean, except for June which is a 2-year (1999-2000) mean.

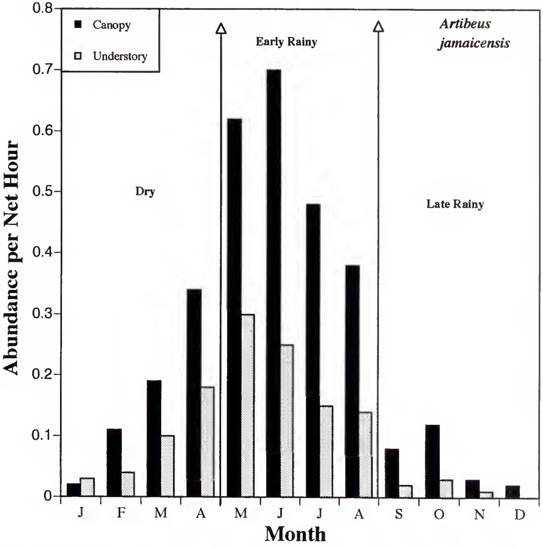


Figure 4-9. Temporal and vertical activity of the large fig-eating bat, *Artibeus jamaicensis* in a lowland forest. Species abundance measured as monthly bats captured per net hour in the forest understory and canopy. Each monthly bar represents a 3-year (1998-2000) mean, except for June which is 2-year (1999-2000) mean.

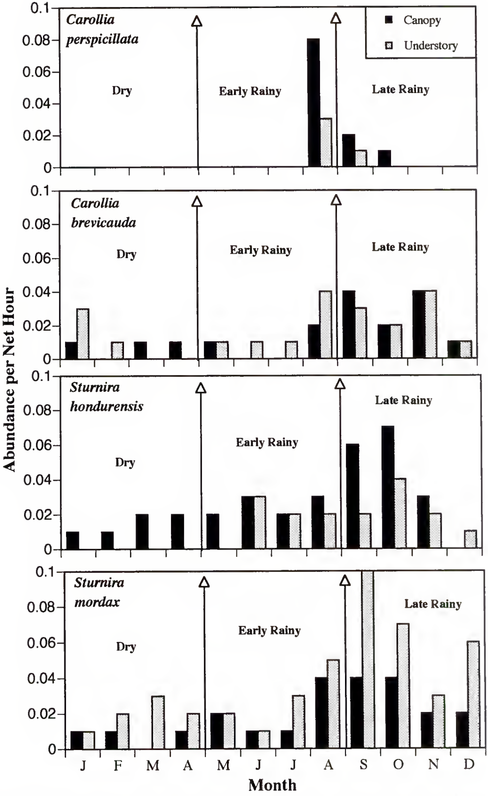


Figure 4-10. Temporal and vertical differentiation of cloud forest *Piper-Solanum* bats, genera *Carollia* and *Sturnira*. Species abundance measured as monthly bats captured per net hour in the forest understory and canopy. Each bar represents a 3-year (1998-2000) mean, except for June and *C. perspicillata*, which are a 2-year (1999-2000) mean.

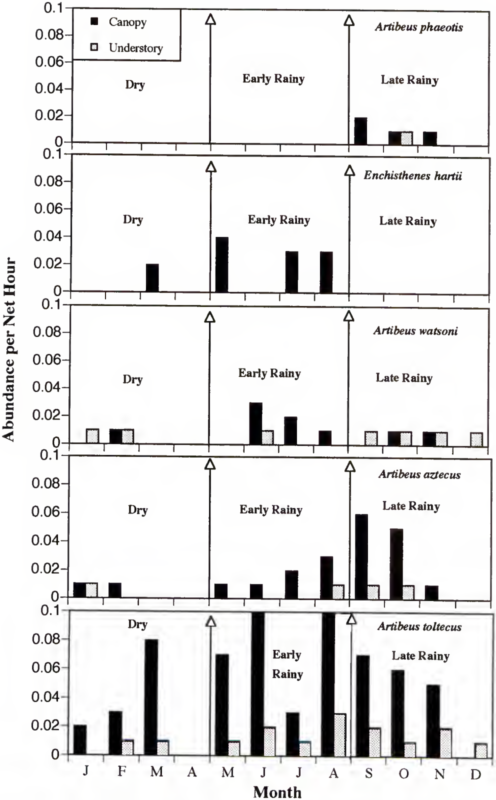


Figure 4-11. Temporal and vertical differentiation of small cloud forest fig-eating bats, genera *Artibeus* and *Enchisthenes*. Species abundance measured as monthly bats captured per net hour in the forest understory and canopy. Each bar represents a 3-year (1998-2000) mean, except for June which is a 2-year (1999-2000) mean.

Table 4-2. Proportion of canopy to understory bat captures by season for cloud forest nectarivorous and frugivorous bats. Proportions were calculated from 3 year-mean (1998-2000) seasonal values of species abundance•.

	Proportion of canopy to understory bat captures			
Species•	Dry season	Early rainy	Late rainy	P*
H. underwoodi	0.6	1.0	2.0	0.05
S. mordax	0.3	0.7	0.5	n. s.
S. hondurensis	15.0	1.5	1.8	0.004
C. brevicauda	0.7	0.4	1.1	n. s.
A. toltecus	4.3	4.4	3.0	n. s.
A. aztecus	2.0	8.5	5.7	n. s.
A watsoni	0.5	6.7	0.5	<0.0001
E. hartii	20.0	33.0	«	n. s.

•Only those species with sample size •40 individuals. •*H.*: *Hylonycteris*, *S.*: *Sturnira*, *C.*: *Carollia*, *A.*: *Artibeus*, and *E.*: *Enchisthenes*. *Likelihood ratio chi-square (G^2). «Species was absent from the site.

Small cloud forest frugivorous bats, *Artibeus* and *Enchisthenes*, maintained the same level of canopy used among seasons (G^2 • 3.2, *df* = 2, *P* • 0.2), except *A. watsoni*, which showed preference for the understory during the dry and late rainy season (G^2=32, *df* = 2, $P < 0.0001$). *Artibeus phaeotis* foraged more in the canopy during its short visit during the late rainy season. Large cloud forest frugivorous bats, *Artibeus* and *Platyrrhinus*, were almost restricted to the canopy (• 85% of captures), in consequence their seasonal abundance distribution (Figure 4- 2) represent also their strata use (Table 4-2, Figures 4-10, 4-11, Appendix B).

Discussion

Early studies on bats have provided only a general pattern of bat vertical habitat differentiation that did not include description of seasonal changes (Bernard 2001, Kalko and Handley 2001, Lim and Engstrom 2001), and have led to the description of bat temporal patterns of species diversity or coexistence without considering bats' differential vertical distribution (Fenton *et al.* 1992, Cosson *et al.* 1999, Medellin *et al.* 2000, Schulze *et al.* 2000, Stoner 2001, but see Bonaccorso 1979). By integrating simultaneous vertical and temporal monitoring of nectarivorous and frugivorous bats in two contrasting forests (Chapter 2) with a similar species composition (Chapter 3), I was able to clearly identify temporal variability in bat vertical stratification.

Temporal and Vertical Stratification Patterns

The abundance of nectar- and fruit-feeding bats varies seasonally and some bat species are specialized to feed on understory or canopy fruits (reviewed by Fleming 1986b, 1992). These observations have allowed to classifying bat species as abundant or rare, and as understory or canopy. However, this study has documented high spatial and temporal variance of bat assemblages, resulting from the ecological flexibility of some species. Some species performed their main activities mostly in the canopy, whereas other species seasonally switched their main activities from one stratum to other. This study indicates that an annual study that samples only in the understory or a vertical segregation study that samples only at certain time will obtain strongly biased results for bat abundance.

The seasonal abundance of lowland and cloud forest plant-visiting bats was not uniform and it related to rainfall. Periods of high capture rates for plant-visiting bats in both forests (May-August, September-October) may had coincided with times of high bat plant production. These months has been documented on Barro Colorado Island in lowland Panamá and in the Monteverde cloud forest in Costa Rica as times of peaks in bat plant production (Bonaccorso 1979, Dinerstein 1983). Differences among species in their seasonal abundance may represent species-specific responses to climate, forest structure, plant phenology, and/or presence of competitors.

The plant food resource available to understory and canopy nectarivorous and frugivorous bats differs in size, quantity, and phenology (Fleming 1988, 1992, Schatz

1990). The spatial and temporal distribution of food resources in the cloud forest may impose constraints in the behavior of these bats by requiring a different foraging strategy from the foraging used in the lowlands (Fleming 1982, 1986b, 1992, Thies 1998). The "guilds" of plant-visiting bats, nectarivorous bats, *Piper-Solanum* bats, small fig-eating bats, and large fig-eating bats were numerically dominated by one or two species. The less dominant species differentiate their activities from the abundance pattern of dominant species. Furthermore, these guilds include a group of species with different migratory behaviors. The presence of migratory species in a bat community might be constrained by both food availability and competitors (Bonaccorso and Humphrey 1984, Bonaccorso and Gush 1987).

Nectarivorous Bats

Food availability and the presence of competitors may influence temporal and vertical distribution of nectar-feeding bats. Of two species of nectarivorous bats found in the lowland forest, *G. soricina* was clearly numerically dominant over *G. commisarissi* (Appendix 2). The food habits of *G. soricina*, which include nectar and a great representation of fruits (Bonaccorso 1979, Fleming 1988, Willig *et al.* 1993), may confer it an advantage for foraging in the understory. *Glossophaga soricina* also has a foraging strategy intermediate to the more specialized frugivorous bats that may allow it to compete with understory frugivorous bats and feed on canopy fruits (Bonaccorso and Gush 1987, Dumont 1999). *Glossophaga* species were found more in the canopy in cloud forests than in the lowlands.

Extensive use of the cloud forest canopy suggests that nectarivorous bats may have had more food resources in this stratum than in the understory. The smaller nectar-feeding bats (*Glossophaga* and *Hylonycteris*) foraged more in the understory than larger species (*Lonchophylla robusta* and *Anoura* spp.). The exception was the small *Lonchophylla mordax* with the two only captures occurring in the canopy. The ecology of this species needs to be investigated to test if its canopy preference is real or whether it represents habitat displacement. Nectarivorous bats in the Iwokrama forest, Guyana differentiated by vertical stratification (Lim and Engstrom 2001). In the cloud forest nectarivorous guild, which comprised seven species, only *H. underwoodi* was present during most of the year. This species was an understory bat during the dry season and a canopy bat during the late rainy season. *Hylonycteris* may have switched from the understory to canopy during the rainy season for nutritional reasons. The few data available on the phenology of cloud forest bat-pollinated plants indicate that they mainly flower during the dry season (Dinerstein 1983).

Nectarivorous bats in the subfamily Glossophaginae generally are smaller than Neotropical frugivorous bats (Fleming 1988, 1992). However, nectar-feeding bats overlap in size with small members of the *Piper-Solanum* frugivorous bats and small fig-eating bats, which may lead to the sharing of food resources among these trophic groups. Fleming (1988) found in a Costa Rican dry forest that the diet of *G. soricina* overlapped with members of the understory guild, *C. perspicillata*. A similar feeding pattern in *G. soricina* was reported in Brasil and México (Willig *et al*. 1993, Herrera *et al*. 1998).

Piper-Solanum **Bats**

Piper-Solanum bats specialize on high-quality nutritional fruits that are available year round (Fleming 1986b, 1988, Thies 1998). Previous studies indicate that minor differences in body size (e. g., *Carollia*) imply causation to segregation by diet, horizontal habitat, and time (Bonaccorso 1979, Fleming 1988, 1991, Thies 1998). In this group, C. *brevicauda* may face a strong selection for differentiating in resource use because it overlapped in both forests with a species of *Sturnira*.

Piper-Solanum bats likely coexist by differing in their temporal and vertical resource use. The four species showed a gradient in strata use, from an understory specialist (*C. castanea*) to a canopy specialist (*S. lilium*). However, within *Carollia* the smaller species used more the understory than larger species. It is possible that *C. perspicillata,* the dominant species, and *C. castanea* maintain their abundance during all seasons because they differentiated by both strata use and the timing of their abundance peaks. The two similarly sized species, *C. brevicauda* and *S. lilium*, were less abundant during the entire year, but the former species was mainly captured in the understory during the last six months, whereas *S. lilium* had more captures during the first half of the year. This pattern of temporal and vertical differentiation among lowland *Piper-Solanum* bats is likely related to differences in their food habits (Bonaccorso 1979, Humphrey and Bonaccorso 1984, Fleming 1988, Marinho-Filho 1991, Willig *et al.* 1993, Thies 1998).

Within the *Piper –Solanum* group, *Carollia* species were captured more frequently in the cloud forest canopy than in the lowland forest canopy, whereas *Sturnira* species had more captures in the cloud forest understory than in the lowlands. It needs to be addressed if these behaviors represent either nutritional requirements of smaller species or habitat displacement by *S. mordax*. These species were captured in the canopy with a different frequency, but it was not related to body size. Nevertheless, the two *Carollia* species had the same trend in canopy use and body size than in the lowlands, with the larger species using more of the canopy than the smaller species. The two dominant species, *S. mordax* and *S. hondurensis*, likely co-occur through a temporal differentiation in strata use, especially during the dry season and the late rainy season, when food resources may be low. *Carollia brevicauda* was mostly captured in the understory when the similarly sized *S. hondurensis* was using the canopy (dry season). *Carollia perspicillata* arrived during the end of the early rainy season, maybe when there is enough food available. *Carollia perspicillata* behaves as a migratory species and its arrival may represent an altitudinal movement because it coincided with a decrease in abundance in the lowland population. Several studies have pointed to *C. perspicillata* as a seasonal migratory species, especially in dry forests (Fleming 1988, Stoner 2001).

Species of *Sturnira* spp. are likely able to coexist with other frugivorous bats because of their intermediate foraging strategy and the consumption of *Solanum* fruit (Dinerstein 1983, 1986, Fleming 1986b, Bonaccorso and Gush 1987, Gorchov *et al.* 1995, Hernández-Conrique *et al.* 1997, Dumont 1999). *Carollia* spp. did not overlap in food preferences with fig-eating bats *Artibeus phaeotis*, *A. jamaicensis*, and *A. lituratus* in a Costa Rican dry forest (Fleming 1988), but *C. perspicillata* overlapped in diet with *A. phaeotis* on Barro Colorado Island moist forest (Bonaccorso and Humphrey 1984).

Small Fig-Eating Bats

Although all small lowland fig-eating bat species had more captures in the canopy, smaller *Artibeus* and *Vampyressa* species used the understory more than larger species. This group of bats had two dominant species (*A. watsoni* and *A. phaeotis*) with similar trends in annual abundance and strata use. The coexistence of these two species of *Artibeus* may be mediated by the differential selection of seasons or habitats based on moisture conditions. In Panamá, *A. phaeotis* is dominant over *A. watsoni* on Barro Colorado Island, but the opposite occurs in wetter Bocas del Toro or in Central American cloud forests (Dinerstein 1983, Kalko *et al.* 1996a, Chapter 3).

Smaller species of cloud forest frugivorous bats were captured more in the understory than larger species. This pattern was also found among the group of closely related small *Artibeus* and *E. hartii*. The behavior of these small species needs to be studied to test if their understory preference response to fruit availability or displacement by small highland specialist bats. The results of this study suggest that temporal differentiation in abundance is an important coexistence mechanism among small fig-eating bats, whereas, vertical differentiation appeared to play a secondary role.

In the cloud forest, also the temporal abundance pattern of less dominant species differed from the abundance pattern of dominant species. For example, *A. aztecus*' abundance peak was during the late rainy season when the dominant species, *A. toltecus*, was decreasing in abundance. The increase in abundance of *A. watsoni* coincided with a period of low abundance in *A. aztecus* during the early rainy season. The two other species of small fig-eating bats analyzed, *E. hartii* and *A. phaeotis*, behave like migratory species, the former was present during the early season, whereas the latter was present during the late rainy season. *Enchisthenes hartii* seems to be a seasonal resident in Monteverde (Dinerstein 1983). *Vampyressa pusilla* showed migratory behavior in both forests (Chapters 2, 3) (see also Humphrey and Bonaccorso 1984). Small fig-eating bats, except *A. toltecus*, were captured more frequent in the understory during the dry season and the late rainy season.

Large Fig-Eating Bats

Fleming (1992) stated that large frugivorous bats no compete among themselves because their food resource is abundant year around. However, studies in Panamá and Brasil suggest that both distribution and abundance of fig species influence bat communities (Kalko 1998). *Artibeus jamaicensis* a fig specialist (Bonaccorso 1979, Handley *et al.* 1991), was by far the most numerically dominant lowland species among frugivorous bats, especially during the beginning of rains, as in other sites (Kalko *et al.* 1996a, Kalko and Handley 2001). This species used the canopy more in this site than in other lowland forests (Bonaccorso 1979, Bernard 2001, Kalko and Handley 2001). Factors such as feeding areas, roosts, and predation (Bonaccorso 1979, Kalko 1998, Kalko and Handley 2001) may influence bat strata use in addition. Large species of *Artibeus* seem to respond to forest structure (Chapter 2): if the understory is too dense, large bats may not be able to fly efficiently, because they lack the maneuverability to avoid close obstacles (Stockwell 2001).

The influence of the understory cover in the use of the strata was more evident in the cloud forest, where all species of large fig-eating bats, genera *Artibeus* and *Platyrrhinus*, foraged mainly in the canopy. Although most of the species had a peak in abundance during June, some temporal differentiation occurred among them. For example, *A. lituratus* extended its abundance to August when the dominant *P. vittatus* had low abundance. *Artibeus jamaicensis* seems to be a seasonal visitor in this forest because it was absent during the dry and the late rainy season. Two peaks in bat fruit availability occurred on Monteverde cloud forest, one on March-May, the other on September-October (Dinerstein 1983, 1986). Only the less abundant species, *A. intermedius*, coexisted with the dominant *P. vittatus* during the entire year. The data from Monteverde suggest a similar temporal differentiation among large frugivorous bats (Dinerstein 1983, Timm and LaVal 2000b).

Studies of the effects of environmental variability on the composition and structure of bat species assemblages are relevant to understanding the importance of biotic interactions such as mutualism, competition, and predation. I have shown that the vertical stratification of nectarivorous and frugivorous bats in the lowland forest was more clearly defined (understory *vs* canopy bats) than in the cloud forest. However, both sites showed seasonal variability in bat vertical stratification. The results from the lowland forest are consistent with the findings of a number of previous studies on bats and other sorts of organisms (Feinsinger 1976, Bonaccorso 1979, Greenberg 1981, Loiselle 1988, Roubik 1993, DeVries *et al.* 1999, DeVries and Walla 2001). Further observations integrating diet and horizontal habitat preferences, are required in other diverse forest types, including human-disturbed habitats, to improve our understanding of resource differentiation in tropical bats.

CHAPTER 5
GENERAL CONCLUSIONS

In spite of early studies in bat vertical stratification (Handley 1967) and community structure (McNab 1971), and later works integrating seasonality (Fleming *et al.* 1972, Thomas 1972, LaVal and Fitch 1977) and strata use (Bonaccorso 1979), the analyses of bat communities is still in its infancy (Kalko 1998). Because of their flying, nocturnal behavior, high diversity, and taxonomic uncertainty, the investigation of bats is more difficult than in most vertebrates (Fenton 1993, Lim and Engstrom 2001). Recent studies confirmed the vertical segregation in lowland bats (Bernard 2001, Kalko and Handley 2001, Lim and Engstrom 2001) and concluded that a lowland bat community varies in species composition through the year (Bonaccorso and Humphrey 1984). However, to understand the factors regulating species diversity, we need to know how spatial-temporal variations in the environment influence the population dynamics of species on a variety of scales (Brown 1995).

This investigation has contributed to our understanding of bat ecology through its 3.5-year long-term study comparing bat diversity and ecology of two communities, a lowland forest and a cloud forest in western Panamá. The results demonstrated that bat communities were highly variable in their diversity and indicated that bats are ecologically flexible in tropical forests. These results also suggest both an individualistic-species response by bats to the environment and that bat communities may fit the pattern of a "Gleasonian" community, as in Neotropical bees and birds, and North American granivorous rodents (Karr and Freemark 1983, Brown and Kurzius 1989, Roubik 1992). This community pattern implies that the distribution of each species in both time and space responds to its own unique set of limits and requirements; each is also relatively independent of other species (Brown and Kurzius 1989). Consequently, in these animal communities their diversity patterns change at spatial and temporal macro- and micro-scales in responds to changes in climate and vegetation (Brown and Kurzius 1989). Additionally, this study demonstrated that bat diversity was higher in a mid-elevation cloud forest than in a lowland forest, in opposition to current view (Fleming 1986a, Patterson *et al.* 1996).

This study concluded that lowland species had a clear differentiation between understory and canopy bats, whereas cloud forest species were canopy bats or used equally both strata. The differentiation of lowland bats by strata was related with taxonomic affiliation and food habits. Within the family Phyllostomidae, species in the subfamilies Phyllostominae and Carolliinae, which feed on gleaning insects and shrub fruits, respectively, were mostly understory bats, whereas species in the subfamily Stenodermatinae, which feed on tree fruits, were canopy bats. The sex ratio of some bat species departed from the expected male to female proportion of 1:1 and varied also with forest type and season, but it was more frequent in cloud forest bats. The differential ecological responses of bat species in these communities may be related to differences in competitors, climate, and forest phenology and structure between these sites. Although both forests had similar annual and seasonal rainfall patterns, the cloud forest had higher annual and monthly amounts of rainfall, and lower mean, maximal, and minimal ambient temperatures. The lowlands has a taller, more closed canopy forest with less understory cover than the cloud forest, and both sites had low basal area.

Local environmental conditions in these forests had less influence on bat species richness than on bat species abundance distribution. This observation is in agreement with the view that bat species richness is influence mainly by regional factors than by local factors (Fleming 1986a, Findley 1993, see Cornell and Karlson1997). These forests had similar bat species and taxonomic richness, and total bat abundance, but differed in species abundance distribution. The similarity in species richness resulted from the replacement in the cloud forest of emballonurids by molossids and vespertilionids, and the replacement of phyllostomines by glossophagines. The differences in species abundance resulted from a more evenly distributed species abundance in the cloud forest bats than in lowland bats. The cloud forest species richness and evenness determined that this forest had higher bat species diversity than the lowlands, supporting the argument that a high diversity will be found at mid elevations (mid-domain effect) (Colwell and Lees 2000).

Forest stratification had greater impact on species abundance than on species richness. This result demonstrates that species abundance was influenced by local conditions at different spatial scales, forests and strata. Species richness by forest strata was similar within and between forests. The similarity in species richness was likely the result of the frequent use of both strata by bats. Bat abundance by strata differed within and between sites, with most individuals captured in the canopy, especially in the cloud forest. Both bat communities had temporal variability that caused annual, seasonal, and monthly differences in species richness and abundance within and between sites, and seem to be related to rainfall patterns.

Bat communities in this study had similar guild representations, except for the absence of small piscivorous, omnivorous, and carnivorous guilds in the cloud forest, and were dominated in both forests by the background cluttered aerial insectivore and the frugivore guilds. As in previous studies, McNab's (1971) niche matrix showed high occupancy of cells by more than one abundant species. The pattern in strata use by bat species can explain in some cases the coexistence of similar species. Niche segregation might also occur at a more fine body size-resource scale, as have been demonstrated in frugivores bats (Fleming 1991). Besides vertical stratification, other ecological factors such as food and roost availability, and temporal activity may promote resource differentiation and reduce competitive interactions.

Nectarivorous and frugivorous bat populations had high spatial and temporal variability within and between these forests. Bat species showed high flexibility regarding the use of strata. Although some species used both strata, they used mainly the understory or the canopy, during different seasons. This variability may be related to rainfall patterns at both sites, suggesting the tracking of food resources by bats (Fleming 1992). The environmental heterogeneity in these forests seems to impose a differential constraint in bat foraging behavior that influences their species composition and structure (Bonaccorso and Humphrey 1984, Fleming 1992). "Guilds" of plant-visiting bats had one or two numerically dominant resident species, some less dominant resident species, and one or two migratory species. This observation opens the possibility that lowland species were conducting seasonal migration to cloud forest. Because of seasonal movements, plant-visiting bats face contrasting climate, food availability, and competitors, which may require morphological, behavioral, and ecological adjustments. The differential bat species response to seasonal variability likely caused variation in the patterns of community composition and structure.

Because of high temporal and spatial variability of bat populations, I recommend caution in the interpretation and comparison of short-term bat studies conducted during less than 12 months or at different years, or studies that only sampled in the understory. These studies may mislead about bat community diversity and abundant, bat species strata use, or species rareness.

APPENDIX A
BAT SPECIES CAPTURED IN A LOWLAND FOREST AND A CLOUD FOREST IN CHIRIQUI, PANAMA

Table A-1. Bat species captured with mist net in the lowland forest of Batipa (95 m) and in the cloud forest of Fortuna (1210 m). Species are distributed by guilds, total abundance (n), percentage of canopy use (Canopy %: C), and sex ratio male:female. An asterik indicates the significant difference for canopy and sex ratio*.

	Lowland Forest			Cloud Forest		
Guild/Species•	n	C%+	Sex	n	C%+	Sex
AI						
S. bilineata	7	*86	0.4			
S. leptura	11	*100	0.8			
P. gymnonotus				1	100	
M. nigricans	2	50		24	***12	*3.0
M. keaysi				4	33	0.3
M. oxyotus				1	0	
E. brasiliensis	5	80	0.7			
E. furinalis	1	0				
R. tumida	3	100	0.5			
GI						
M. microtis	8	*12	0.7	1	0	
M. minuta	8	67	2.0			
M. hirsuta	12	25	0.8	1	100	
M. schmidtorum	1	100				
G. sylvestris	7	37	3.0			
T. silvicola	20	*25	*0.6			
M. crenulatum	13	38	1.4			
T. cirrhosus				1	0	
C						
C. auritus	1	0				
O						
L. brachyotis	3	33	2.0			
T. nicefori	3	67	0.5			
P. hastatus	47	***85	0.5			

Table A-1. continued

	Lowland forest			Cloud forest		
Guild/Species•	n	C %+	Sex ratio	n	C %+	Sex
N						
P. discolor	9	67	*0.1	1	100	
G. commissarisi	12	42	0.8	2	50	
G. soricina	101	**33	0.7	10	60	2.0
A. geoffroyi				11	75	1.7
A. cultrata				3	100	
H. underwoodi				47	55	*0.1
L. mordax				2	100	
L. robusta				9	*89	2.0
PF						
C. castanea	131	***14	0.9			
C. brevicauda	61	***25	0.7	131	43	1.0
C. perspicillata	225	**41	1.0	61	**72	*0.47
S. lilium	54	**67	1.1			
S. hondurensis				198	*58	*0.4
S. mordax				224	**35	0.8
SFF						
A. phaeotis	131	***68	*0.7	22	60	0.5
A. watsoni	119	***69	1.3	42	61	0.9
A. toltecus				279	***77	1.2
A. aztecus				106	***78	0.8
E. hartii				57	***85	*0.5
U. bilobatum	20	***90	0.6			
P. helleri	22	***90	*0.4	2	100	2 fem
C. villosum	7	*87	2.5			
C. trinitatum				1	0	1 fem
V. nymphaea	7	62	0.7	20	**75	1.0
V. pusilla	6	83	1.5	19	63	0.6
E. macconnelli				2	50	2 fem
C. senex				1	0	1 fem
LFF						
A. jamaicensis	851	***70	*0.4	115	***89	*2.2
A. intermedius	5	80	0.7	105	***85	1.3
A. lituratus	2	100	2 fem	183	***86	*0.5
P. vittatus				210	***93	0.8
H						
D. rotundus	50	***15	0.8			

Table A-1. continued

AI: aerial insectivores, *S.*: *Saccopteryx*, *P.*: *Pteronotus*, *M.*: *Myotis*, *E.*: *Eptesicus*, *R.*: *Rogheessa*; GI: gleaning insectivores, *M.*: *Mycronycteris*, *G.*: *Glyphonycteris*, *T.*: *Tonatia*, *M.*: *Mimon*, *T.*: *Trachops*; C: carnivores, *C.*: *Chrotopterus*; O.: omnivores. *L.*: *Lamrponycteris*, *T.*: *Trinycteris*, *P.*: *Phyllostomus*; N: nectarivores; *P.*: *Phyllostomus*, *G.*: *glossophaga*, *A.*: *Anoura*, *H.*: *Hylonycteris*, *L.*: *Lonchophylla*; PF: *Piper* frugivores, *C.*: *Carollia*, *S.*: *Strunira*; SFF: small fig frugivores, *A.*: *Artibeus*, *E.*: *Enchisthenes*, *U.*: *Uroderma*, *P.*: *Platyrrhinus*, *Ch.*: *Chrioderma*, *V.*: *Vampyressa*, *E.*: *Ectophylla*, *C.*: *Centurio*; LFF: large fig frugivore, *A. Artibeus*, *P*: *Platyrrhinus*; Haematophagous, *D.*: *Desmodus*. *$P < 0.05$, **$P < 0.01$, ***$P < 0.0001$.

APPENDIX B

BATS SPECIES RECORDED IN A LOWLAND FOREST AND A CLOUD FOREST IN CHIRIQUI, PANAMA

Table B-1. Distribution of bat species by guilds, families and subfamilies, body mass (M), bat abundance (N), and percentage of canopy captures (C%). Species were recorded with combined methods of mist netting and acoustic inventory. The list also includes species from previous inventories.

Guild/Species❖	Fam/Sub-family◆	Lowland Forest M (g)	Lowland Forest N✪	Lowland Forest C%⌖	Cloud Forest M (g)	Cloud Forest N✪	Cloud Forest C%⌖
US/AI (6 species)							
D. albus▫	EMB/Dic	*15.5	▲----	----			
M. ater▫	MOL	*32.5	----	----	*32.5	----	----
M. molossus▫	MOL	*12.0	----	----	*12.0	----	----
N. laticaudatus▫	MOL	*12.6	----	----			
T. brasiliensis▫	MOL				*10.5	----	----
E. glaucinus◆▫	MOL				*38.0	----	----
BCS/AI (20 species)							
S. bilineata▫	EMB/Emb	7.6	7	86 c	*7.6	----	----
S. leptura▫	EMB/Emb	5.1	11	100c			
C. maximiliani▫	EMB/Emb	*4.8	----	----			
Cor. brevirostris▫	EMB/Emb	*9.1	----	----			
P. macrotis▫	EMB/Emb	*5.5	----	----	*5.5	----	----
P. kappleri▫	EMB/Emb	*7.5	----	----			
N. albiventris	NOC	*30.7	----	----			
Pt. gymnonotus▫	MOR	*17.0	----	----	17.0	1	100
M. albescens▫	VES	*6.5	----	----			
M. nigricans▫	VES	7.0	2	50 b	5.3	24	12 u
M. keaysi▫	VES	*5.0	----	----	5.0	4	33 u
M. riparius▫	VES				5.2	----	----
M. oxyotus	VES				6.0	1	0
E. brasiliensis▫	VES	10.6	5	80 c	*10.6	----	----
E. furinalis▫	VES	11.0	1	0	*11.0	----	----
E. fuscus▫	VES				*13.5	----	----
Lasiurus ega▫	VES	*11.0		----	*11.0		
L. cinereus▫	VES						
R. tumida▫	VES	4.7	3	100c	*4.7		

Table B-1. continued

Guild/Species❖	Fam/Sub-family◆	Lowland forest			Cloud forest		
		M (g)	No	C%⊕	M (g)	No	C%⊕
T. tricolor	THY				*4.0	----	----
HCS/AI (1 species)							
P. parnellii¤	MOR	*23.4	----	----	*23.4	----	----
HCS/GI (8 species)							
M. microtis	PHY/Phy	6.6	8 u	12 u	10.0	1 r	0
M. minuta	PHY/Phy	8.0	8 u	67 c			
M. schmidtorum	PHY/Phy	8.0	1 r	100	*8.0	----	----
G. sylvestris	PHY/Phy	8.8	7 u	37 b			
M. hirsuta	PHY/Phy	14.9	12 u	25 u	15.0	1 r	100
M. crenulatum	PHY/Phy	15.1	13 u	38 b			
T. silvicola	PHY/Phy	27.1	20 u	25 u			
T. cirrhosus	PHY/Phy				26.0	1 r	0
HCS/GO (3 species)							
L. brachyotis	PHY/Phy	11.0	3 r	33 u			
T. nicefori	PHY/Phy	11.0	3 r	67 c			
P. hastatus	PHY/Phy	115	47 c	85 c			
HCS/GC (1 species)							
C. auritus	PHY/Phy	78.0	1 r	0			
HCS/GP (1 species)							
N. leporinus	NOC	*55.3	----	----			
HCS/GS (1 species)							
D. rotundus	PHY/Des	32.4	50 c	15 u	*32.4	----	----
HCS/GN (8 species)							
G. commissarisi	PHY/Glo	9.2	12 u	42 b	8.0	2 r	50 b
G. soricina	PHY/Glo	10.1	100a	33 u	9.1	10 u	60 b
H. underwoodi	PHY/Glo				8.4	47 c	55 b
L. mordax	PHY/Glo				9.0	2 r	100c
L. robusta	PHY/Glo				13.1	9 u	89 c
A. geoffroyi	PHY/Glo				15.8	11 u	75 c
A. cultrata	PHY/Glo				21.0	3 r	100c
P. discolor	PHY/Phy	43.2	9 u	67c	42.0	1 r	100
HCS/GF (24 species)							
C. castanea	PHY/Car	13.4	131a	14 u	*13.4	----	----
C. brevicauda	PHY/Car	18.3	61 c	25 u	17.8	131a	43 b
C perspicillata	PHY/Car	19.4	225a	41 b	20.2	61 c	72 c
S. lilium	PHY/Ste	17.8	54 c	67 c	*17.8	----	----
S. hondurensis	PHY/Ste				20.7	198a	58 b
S. mordax	PHY/Ste				27.4	224a	35 u
A. phaeotis	PHY/Ste	11.3	131a	68 c	12.3	22 u	60 b

Table B-1. continued

		Lowland forest			Cloud forest		
Guild/Species❖	Fam/Sub-family◆	M (g)	No✪	C%⌖	M (g)	No✪	C%⌖
HCS/GF (24 species)							
A. watsoni	PHY/Ste	10.9	119a	69 c	12.5	42 c	61 b
A toltecus	PHY/Ste				15.2	279a	77 c
A. aztecus	PHY/Ste				16.5	106c	78 c
A. jamaicensis	PHY/Ste	47.8	851s	70 c	52.8	115a	89 c
A. intermedius	PHY/Ste	60.2	5 r	80 c	63.8	105c	85 c
A. lituratus	PHY/Ste	74.5	2 r	100c	66.8	183a	86 c
E. hartii	PHY/Ste				16.6	57 c	85 c
U. bilobatum	PHY/Ste	17.1	20 u	90 c			
P. helleri	PHY/Ste	14.9	22 u	90 c	16.5	2 r	100c
P. vittatus	PHY/Ste				52.5	210a	93 c
V. caraccioli	PHY/Ste	21.0	1 r	----			
Ch. villosum	PHY/Ste	23.2	7 u	87 c			
Ch. trinitatum	PHY/Ste				*13.0	1 r	0
Ec. macconnelli	PHY/Ste				10.0	2 r	50 b
Va. pusilla	PHY/Ste	9.0	6 u	83 c	9.4	19 u	63 b
Va. nymphaea	PHY/Ste	13.3	7 u	62 c	13.2	20 u	75 c
Ce. senex	PHY/Ste				*20.5	1 r	0

❖US/AI: uncluttered space aerial insectivore- *D.*: *Diclidurus*, *M*: *Molossus*, *N*: *Nyctinomops*, *T.*: *Tadarida*, *E*: *Eumops*. BCS/AI: background cluttered space aerial insectivore- *S.*: *Saccopteryx*, *C*: *Centronycteryx*, *Cor.*: *Cormura*, *P.*: *Peropteryx*, *N.*: *Noctilio*, *Pt.*: *Pteronotus*, *M.*: *Myotis*, *E.*: *Eptesicus*, *L.*: *Lasiurus*, *R.*: *Rhogeessa*, *T.*: *Thyroptera*. HCS/AI: highly cluttered space aerial insectivore- *Pt.*: *Pteronotus*. HCS/GI: highly cluttered space gleaning insectivore- *M.*: *Micronycteris*, *G.*: *Glyphonycteris*, *Mi.*: *Mimon*, *T.*: *Tonatia*, *Tr.*: *Trachops*. HCS/GC: highly cluttered space gleaning carnivore- *C.*: *Chrotopterus*. HCS/GP: highly cluttered space gleaning piscivore- *N.*: *Noctilio*. HCS/GS: highly cluttered space- *D.*: *Desmodus*. HCS/GN: highly cluttered space gleaning nectarivore- *G.*: *Glossophaga*, *H.*: *Hylonycteris*, *L.*: *Lonchophylla*, *A.*: *Anoura*, *P.*: *Phyllostomus*. HCS/GF: highly cluttered space gleaning frugivore- *C.*: *Carollia*, *S.*: *Sturnira*, *A.*: *Artibeus*, *E.*: *Enchisthenes*, *U.*: *Uroderma*, *P.*: *Platyrrhinus*, *V.*: *Vampyrodes*, *Ch.*: *Chiroderma*, *Ec.*: *Ectophylla*, *Va.*: *Vampyressa*, *Ce.*: *Centurio*. ▫Acoustic inventory (Müller 2001). ◆Family/subfamily- VES: Vespertilionidae; MOR: Mormoopidae; MOL: Molossidae; THY: Thyropteridae; NOC: Noctilionidae; EMB: Emballonuridae, Emb: Emballoruninae, Dic: Diclidurinae; PHY: Phyllostomidae, Car: Carolliinae, Glo: Glossophaginae, Ste: Stenodermatinae, Des: Desmodontinae. *Body mass reported from the literature or from the other study site. ⅄----: no data available. ✪Abundance category- r: rare, u: uncommon, c: common, a: abundant, s: superabundant. ⌖Strata use- b: both strata, u: understory, c: canopy

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BIOGRAPHICAL SKETCH

Rafael Samudio Fernández was born on December 11, 1956, in Panamá City, Republic of Panamá. He attended high school at the "glorious eagles nest," the Instituto Nacional, where he received his education in natural sciences as well as philosophical and political formation. He earned a bachelor's degree in biology, specializing in zoology, from the Universidad de Panamá. He works mainly with bats and terrestrial mammals. From 1982 to 1989, he worked for the Ministry of Agriculture and Livestock Development, in the Ecology and Wildlife Diseases section.

His field and laboratory experience with mammals turned his attention to the patterns and processes related to evolutionary ecological adaptations. That interest brought him to the Zoology department at the University of Florida in January 1990 where he enrolled as a postbaccalaureate student. In August 1990 he began his master's program under the guidance of B. K. McNab. After completing his master's degree in 1995, he went on to pursue a Ph.D. in Zoology. Rafael's doctoral study integrated physiological and community ecology to understand the origin, maintenance, and conservation of biodiversity (especially in birds and mammals). While conducting his doctoral research in Panama, he organized the Panamanian Mammal Society, advised bachelor and graduate theses, and was appointed as the coordinator of the Panamanian Program in Ecology and Biodiversity Conservation. Rafael's goal is to return to his country to pursue a carrer including both teaching and research. He hopes to contribute to the scientific and conservation development of his country and the improvement of the next generation of Panamanian biologists.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Brian K. McNab, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Douglas J. Levey
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